Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R(1)*, Brigolin D.(1), Petrizzo A.(1), Zucchetta M.(2),

(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, EXT, is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently "good" model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat "in the middle" between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. ‘Birthday effect’ on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

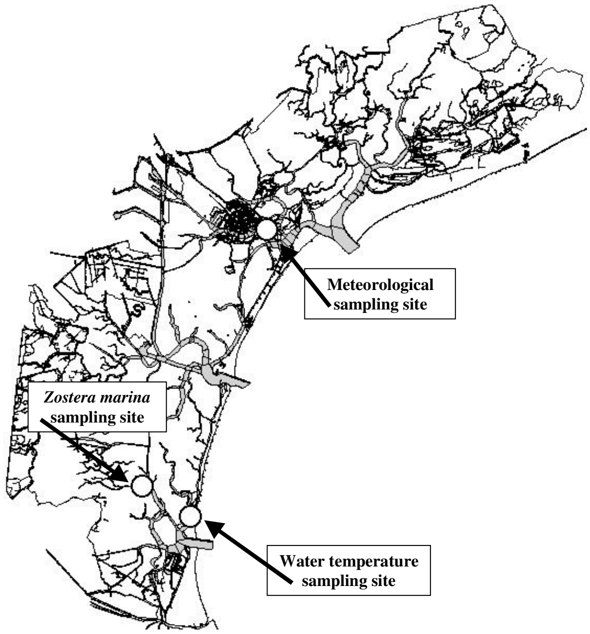

Figure 1. Data sampling sites

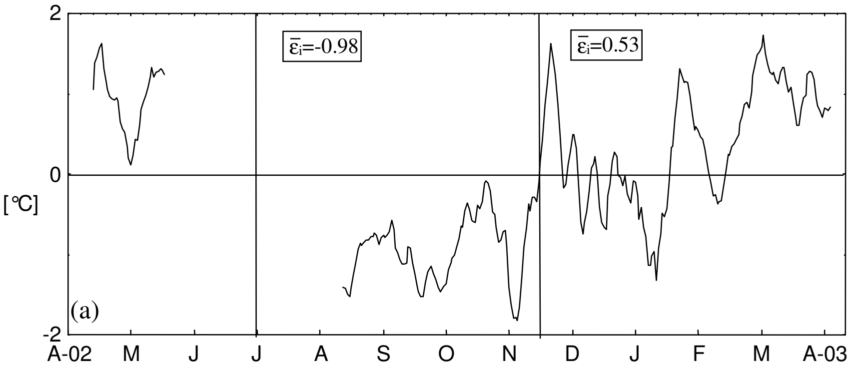

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

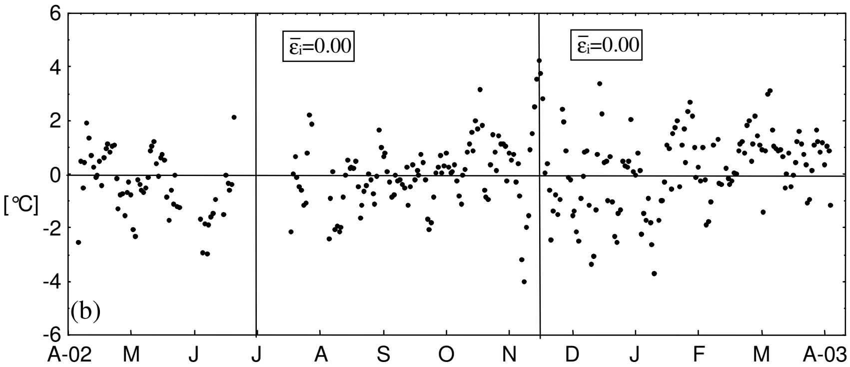

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

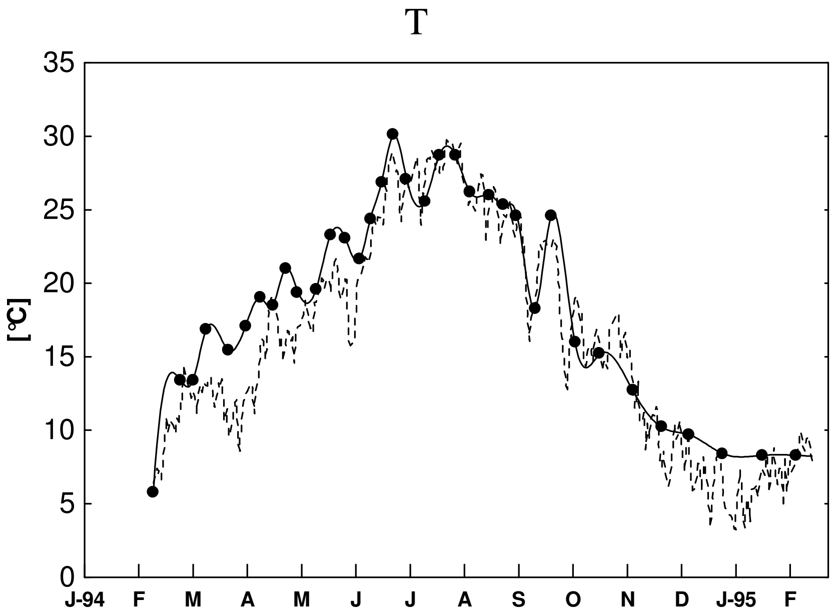

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

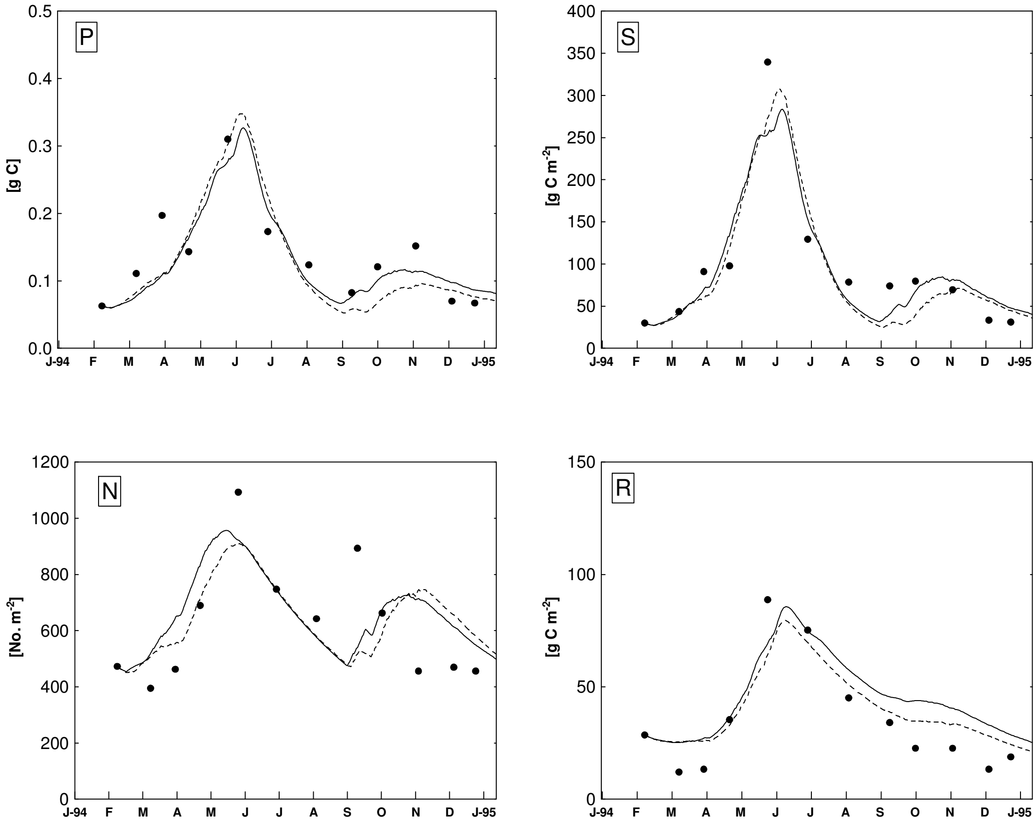

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

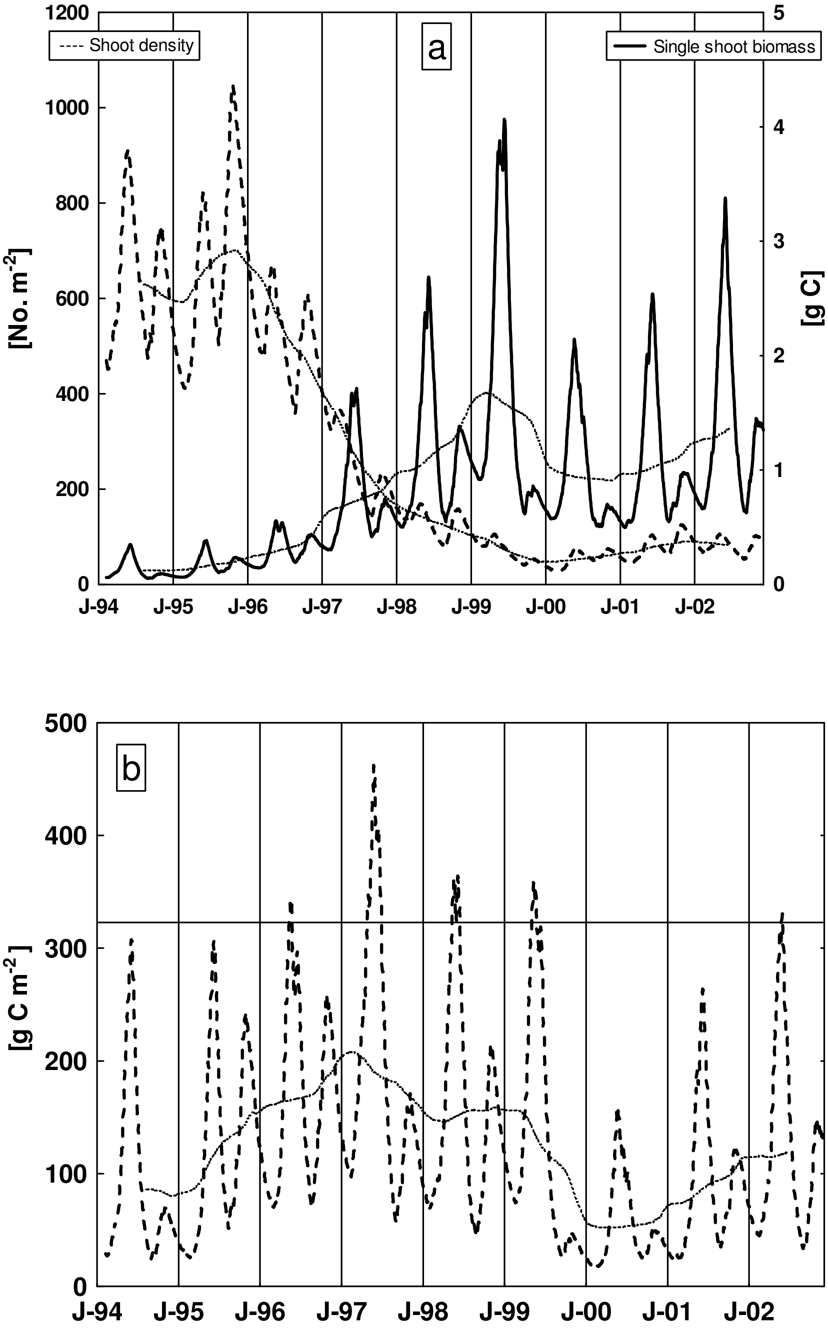

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

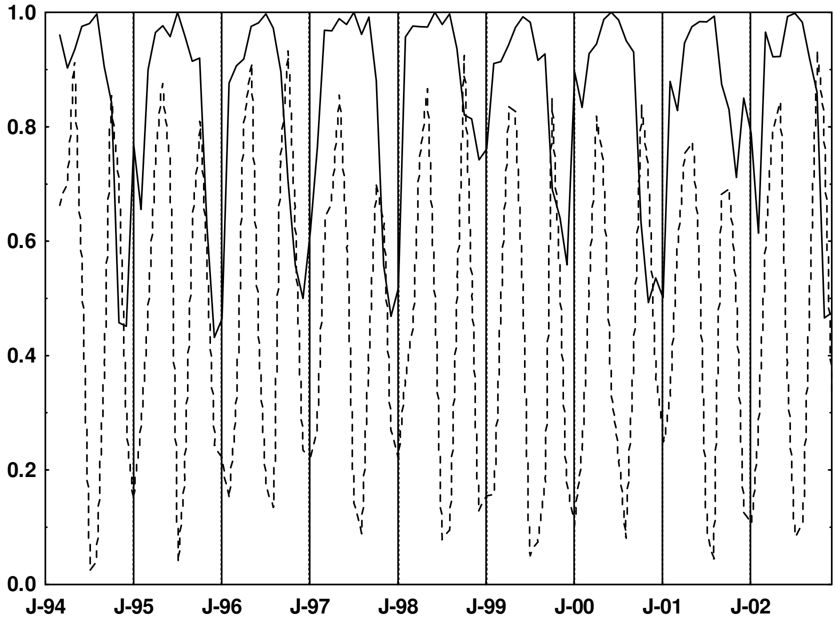

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}^{\ \alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\ \beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}^{\ \gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\ \delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	$\varepsilon_i^{\,2}/N$
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	1x10^{-5} day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R[(1)]*, Brigolin D.[(1)], Petrizzo A.[(1)], Zucchetta M.[(2)],

[(1)]Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
[(2)]Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\dfrac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently "good" model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

Acknowledgements

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

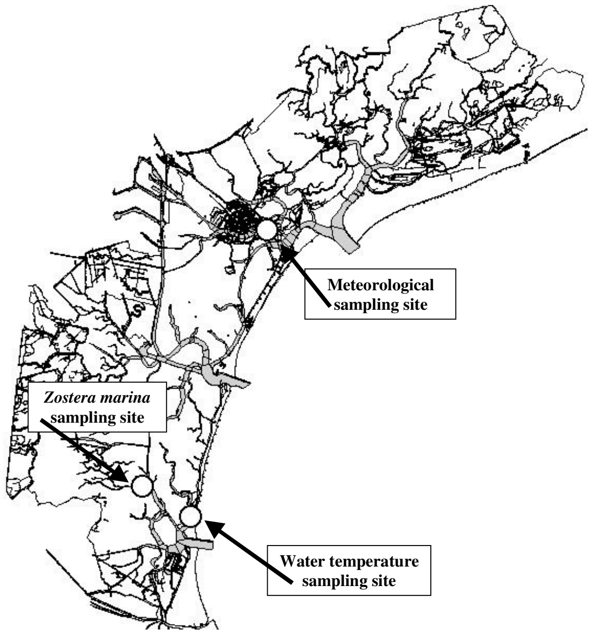

Figure 1. Data sampling sites

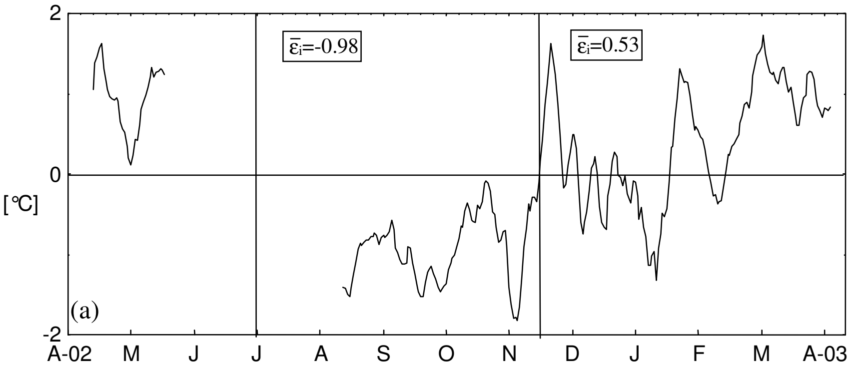

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

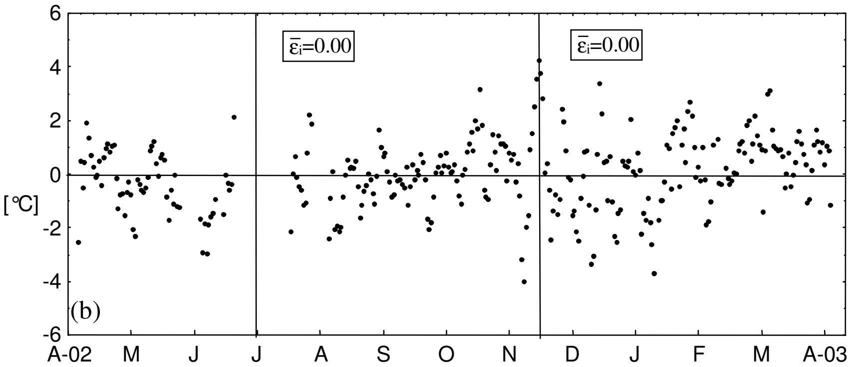

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

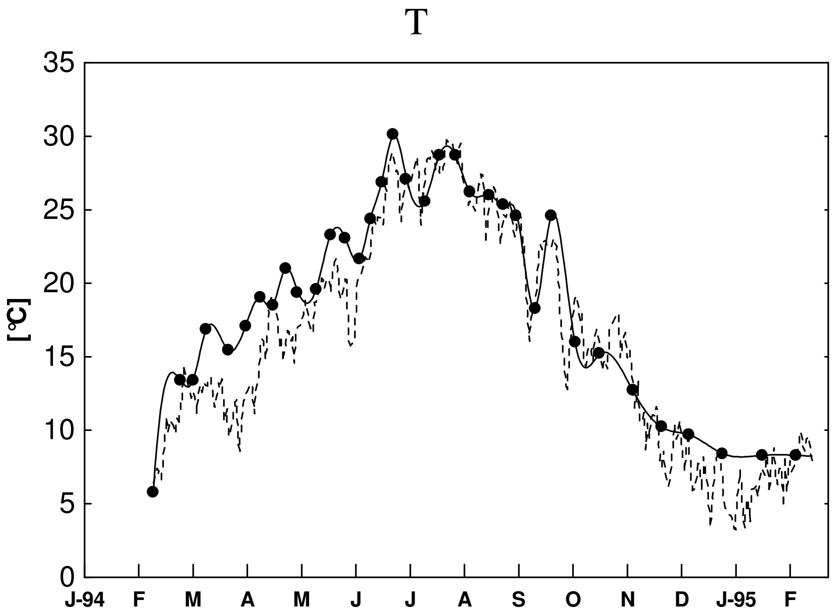

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

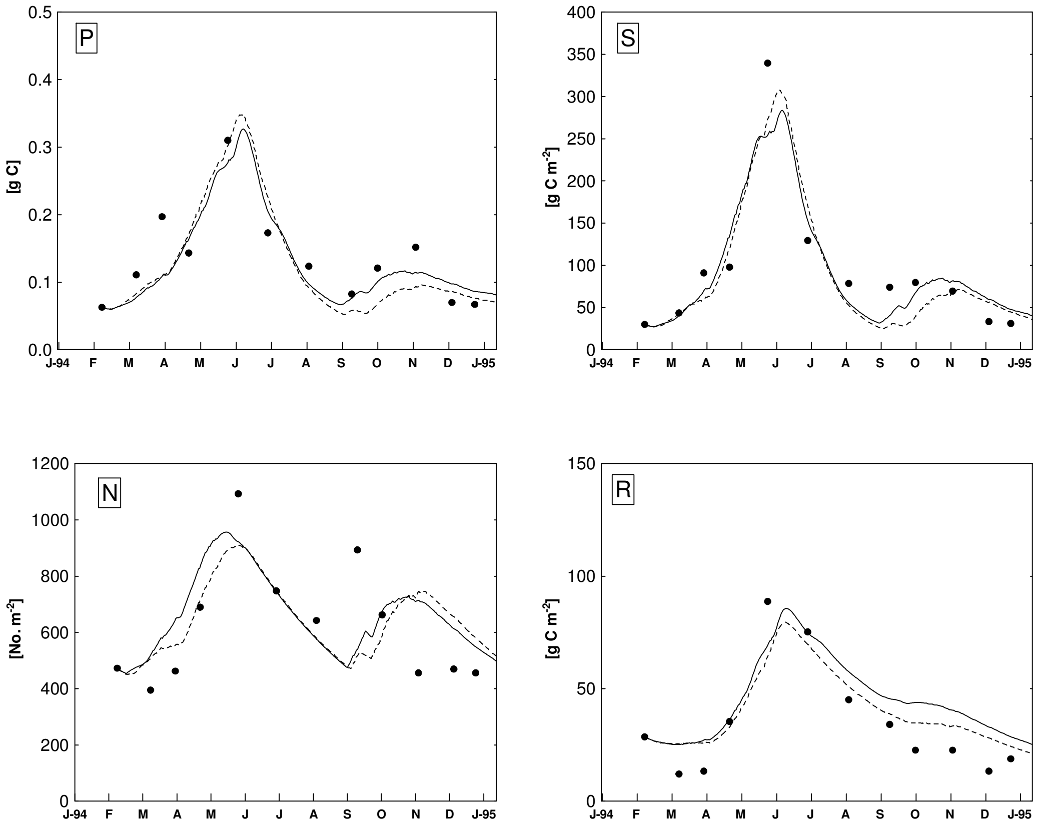

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

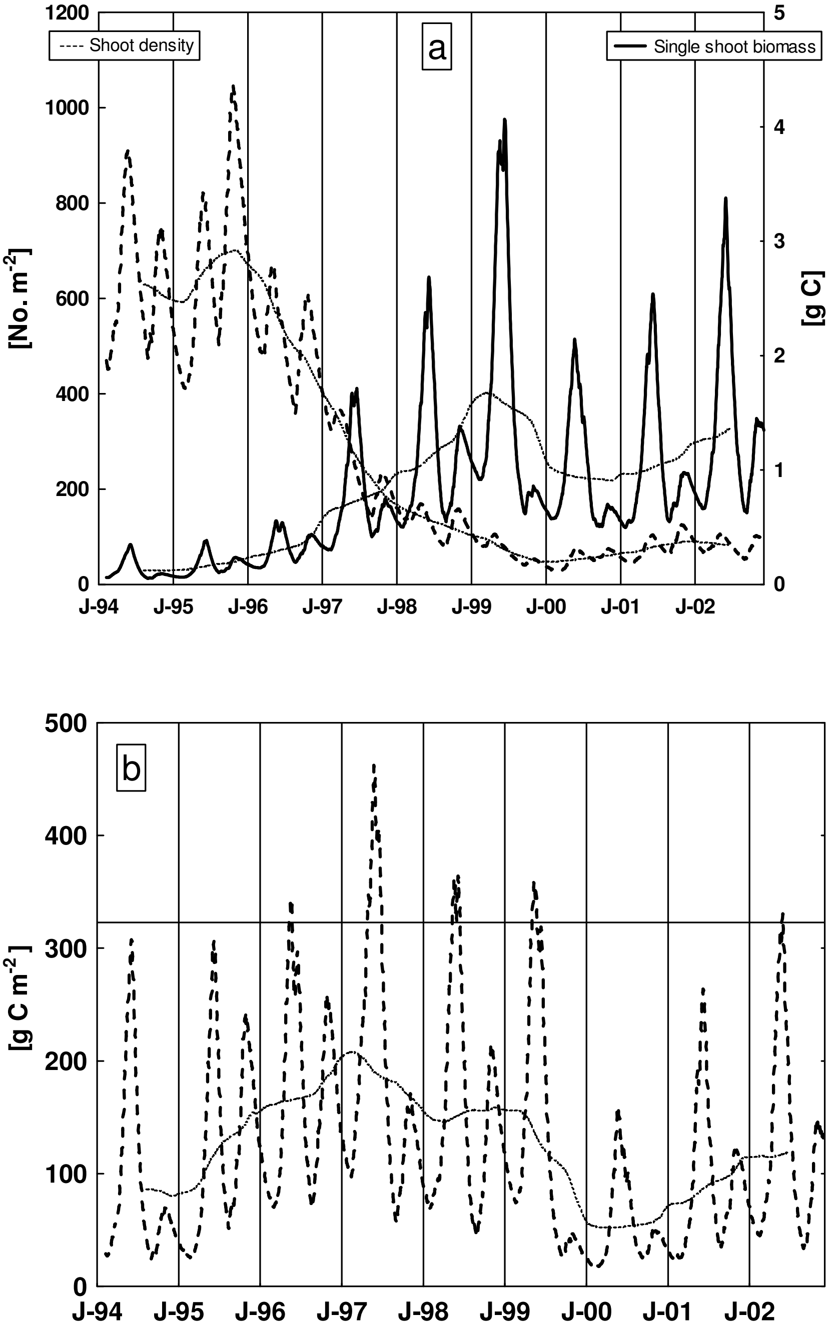

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

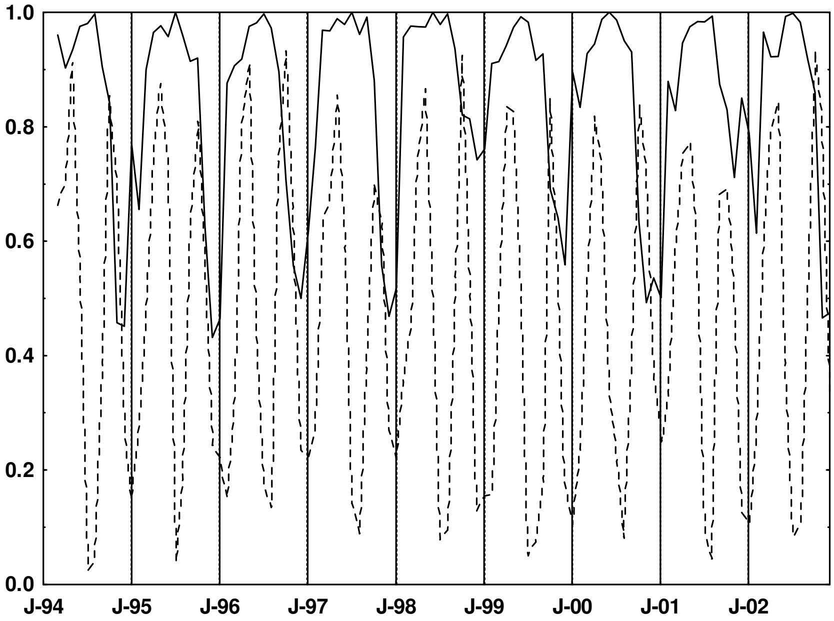

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}\left(T_w\right) = \begin{cases} k_{0\_phot}{}^{\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}{}^{\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}}\right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}}\right)^{stt\_phot}$$

$$f_{\_prod}\left(T_w\right) = \begin{cases} k_{0\_prod}{}^{\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}{}^{\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}}\right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}}\right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma}\right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec\,(T) = \theta_L^{T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	$\varepsilon_i^{\,2}/N$
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	1x10^{-5} day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R$^{(1)}$*, Brigolin D.$^{(1)}$, Petrizzo A.$^{(1)}$, Zucchetta M.$^{(2)}$,

$^{(1)}$Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
$^{(2)}$Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently “good” model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

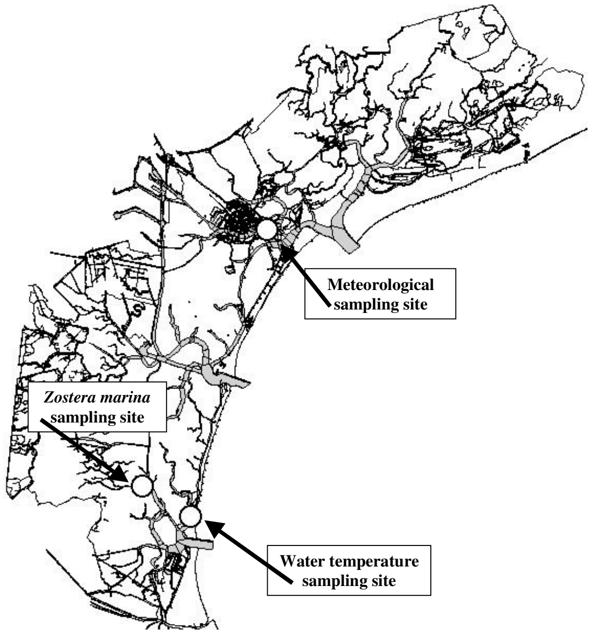

Figure 1. Data sampling sites

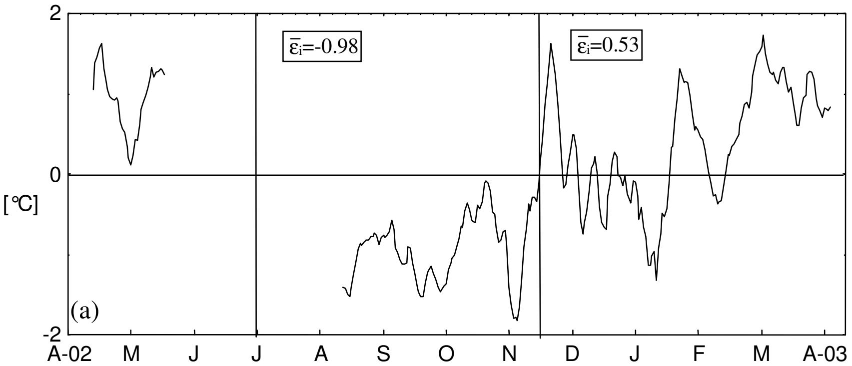

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

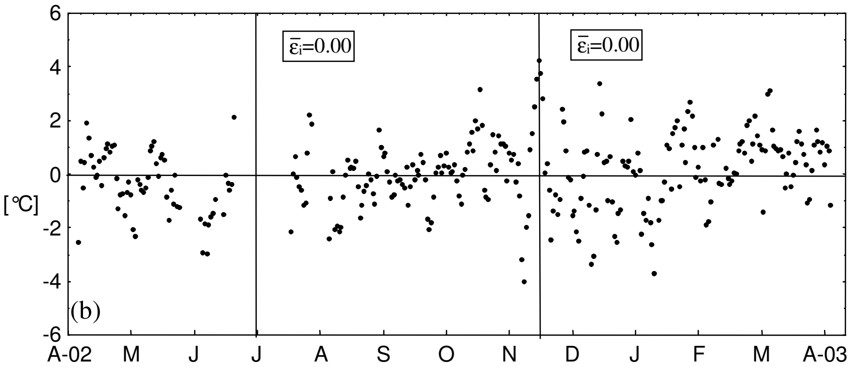

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

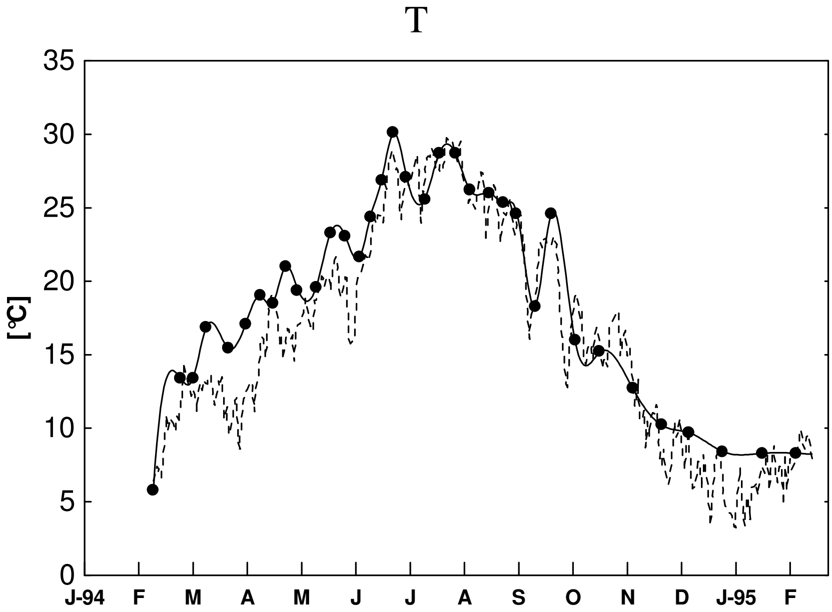

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

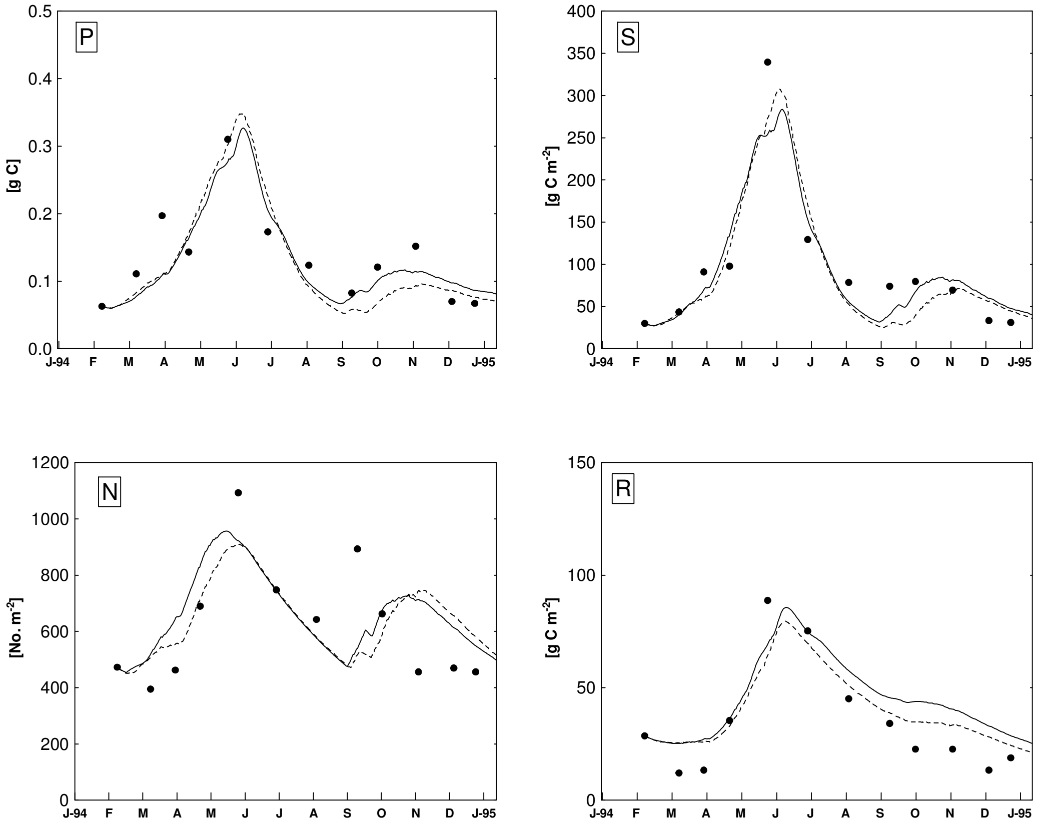

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

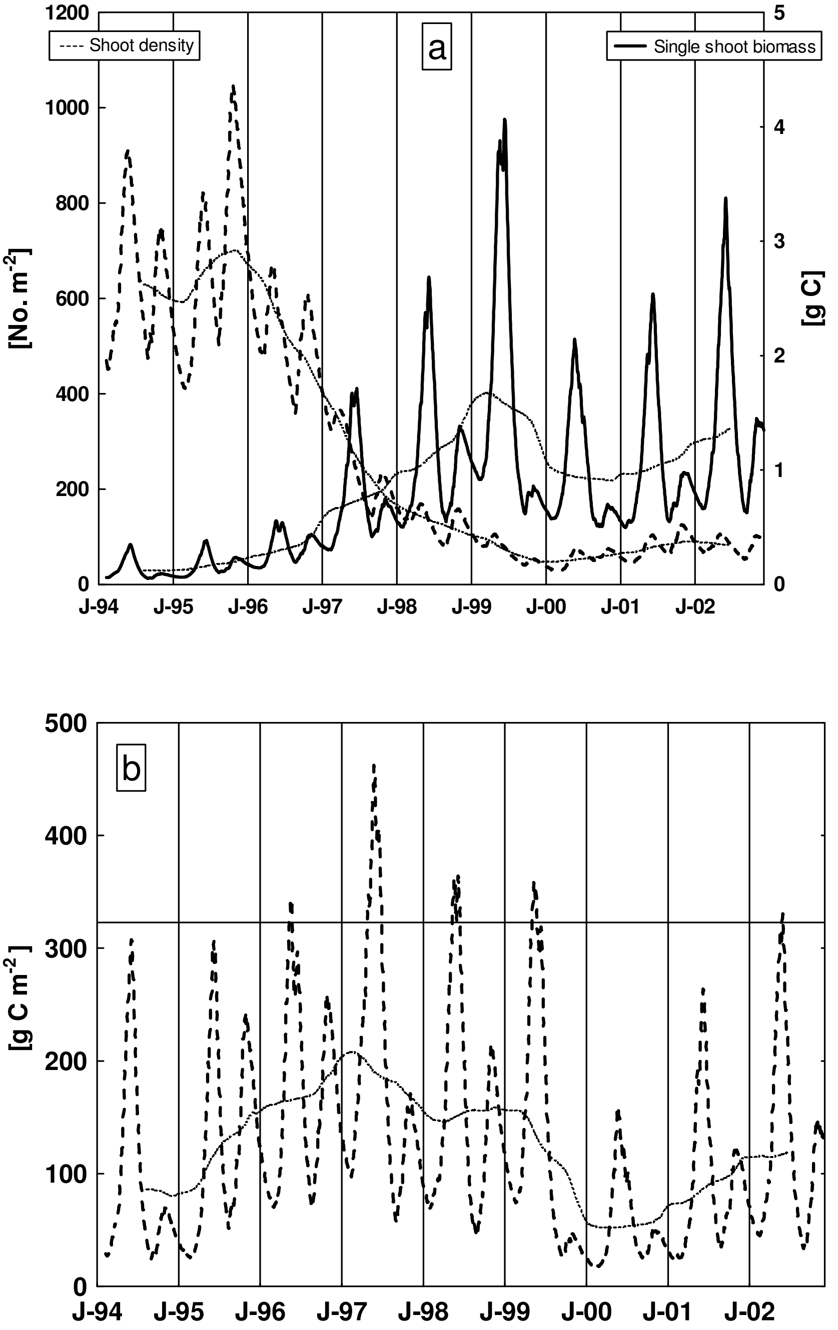

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

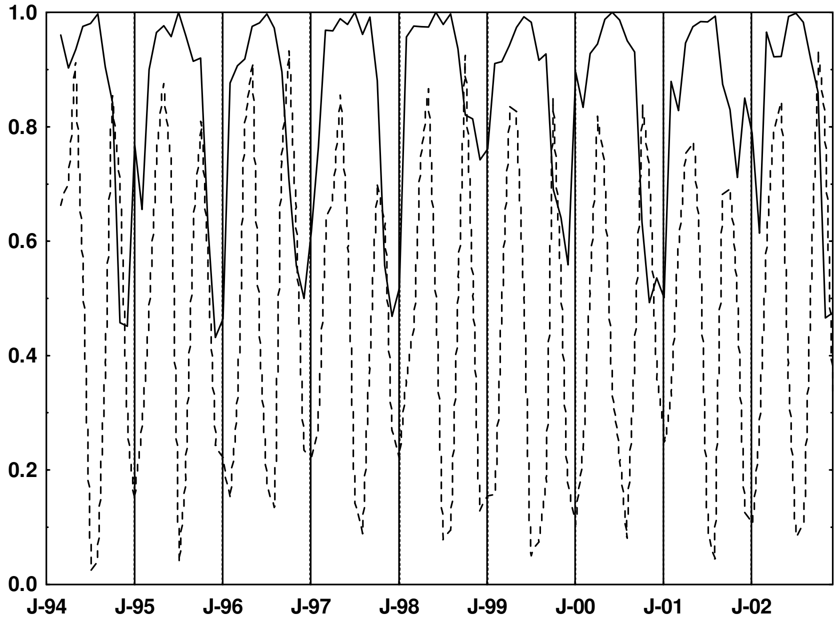

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}{}^{\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}{}^{\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}{}^{\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}{}^{\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	ε_i^2/N
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1x10^{-5}$ day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R(1)*, Brigolin D.(1), Petrizzo A.(1), Zucchetta M.(2),

(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as "archives of hypothesis", since the model structure and our "a priori" estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The "calibration" procedure establishes a relationship between the "theory" and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the "unobserved components" (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j}(\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j}(y_{i,j} - \bar{y}_j)^2}{(n-1)}} \tag{3}$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently “good” model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. ‘Birthday effect’ on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

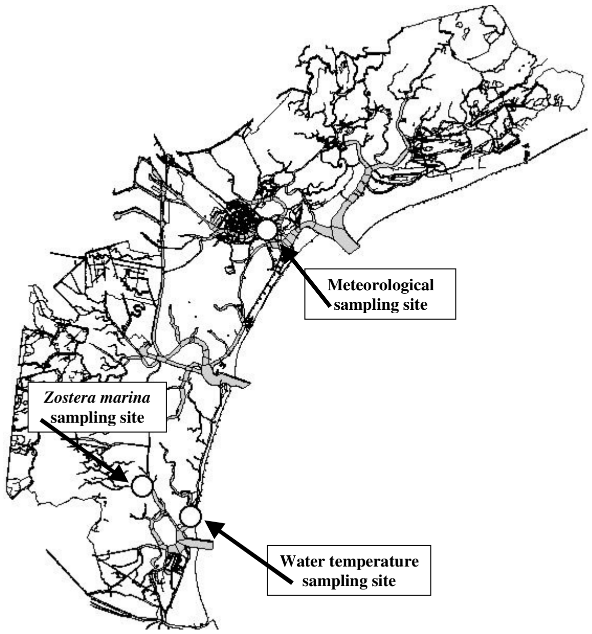

Figure 1. Data sampling sites

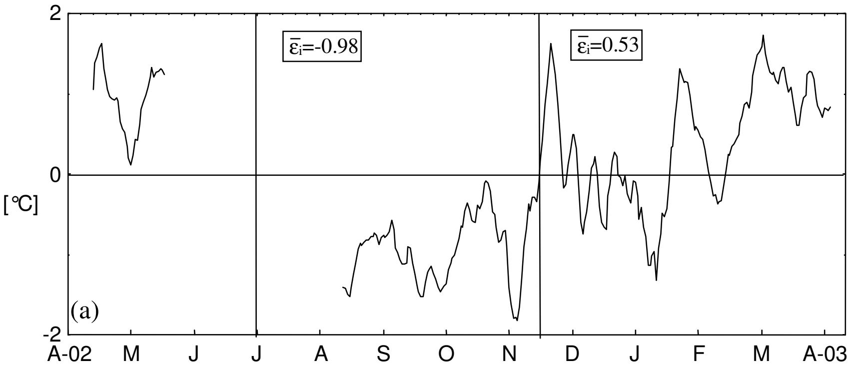

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

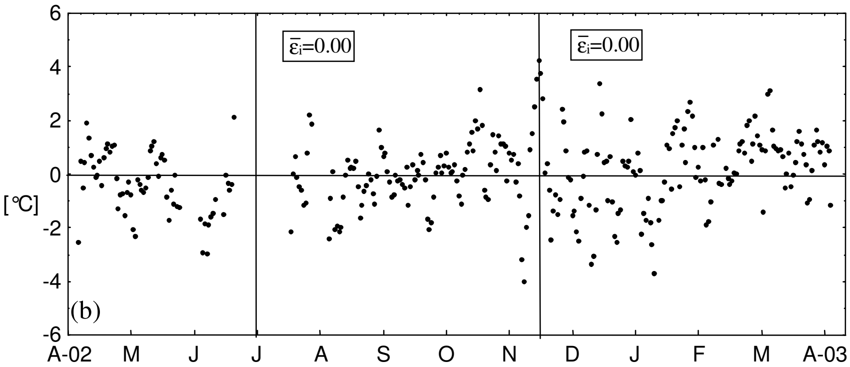

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

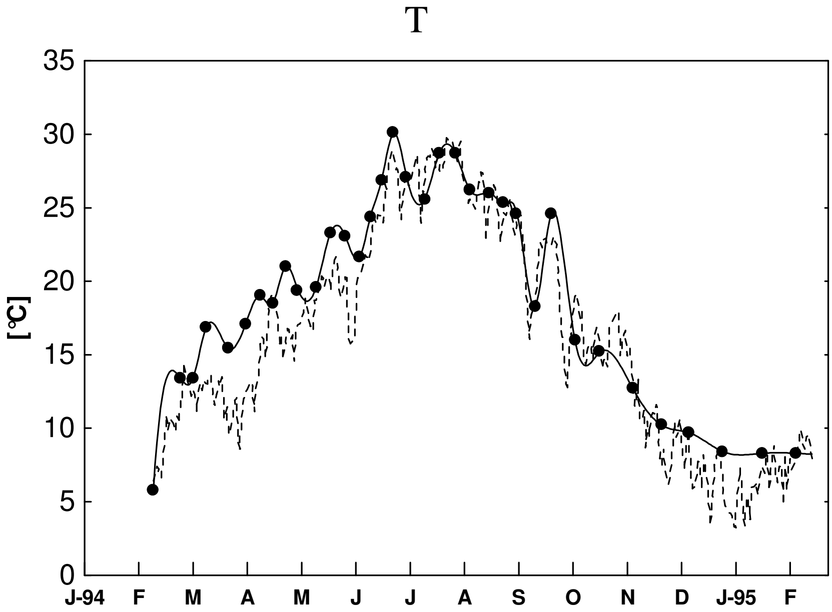

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

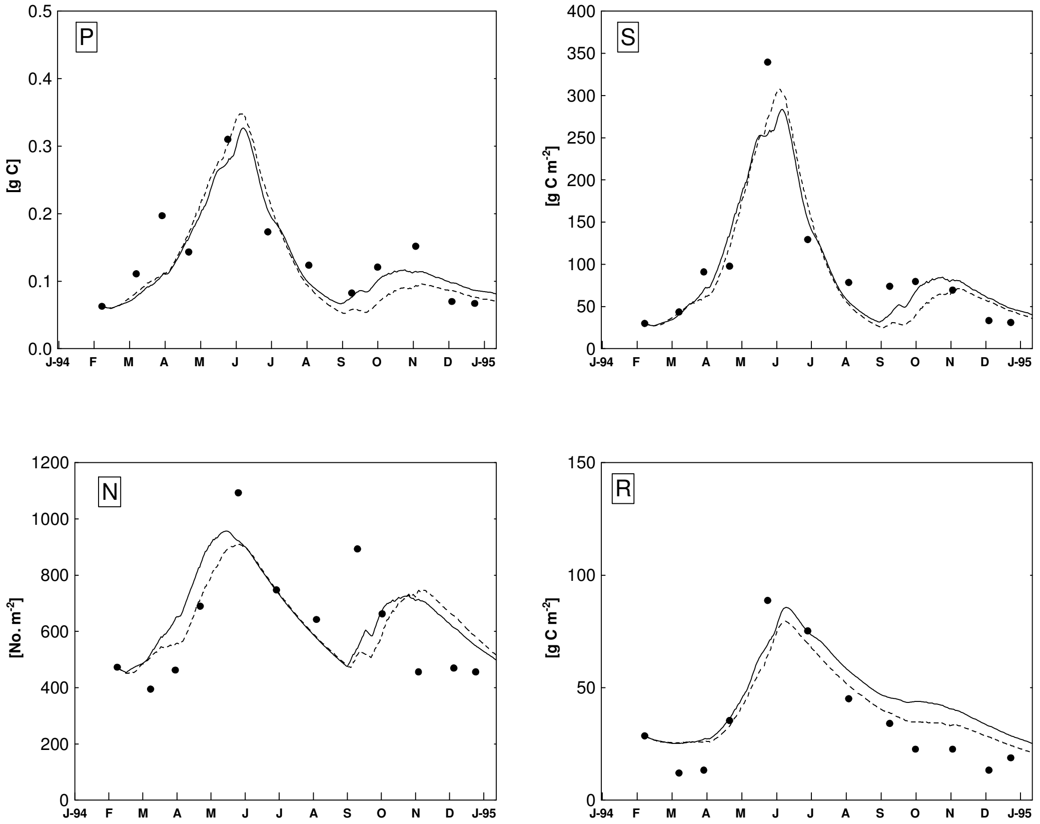

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

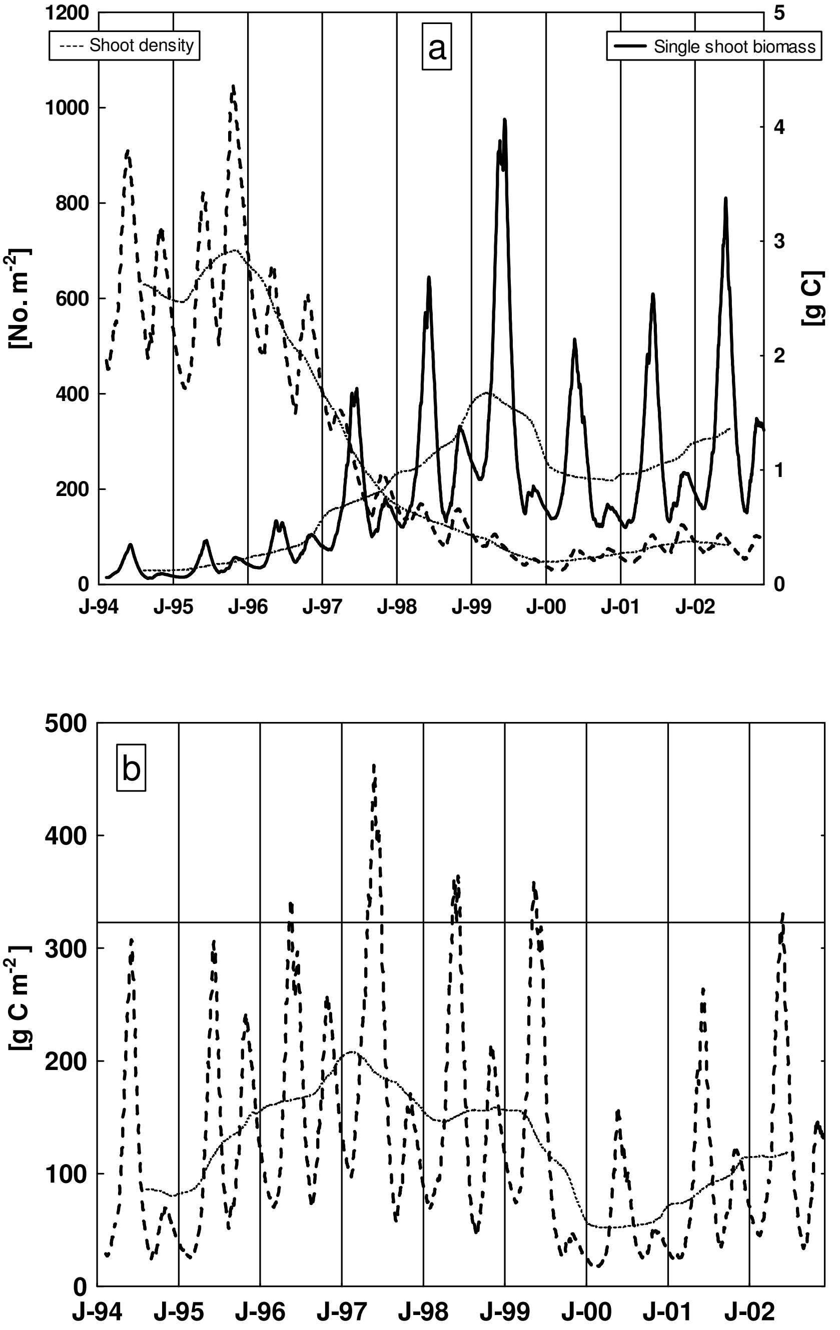

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

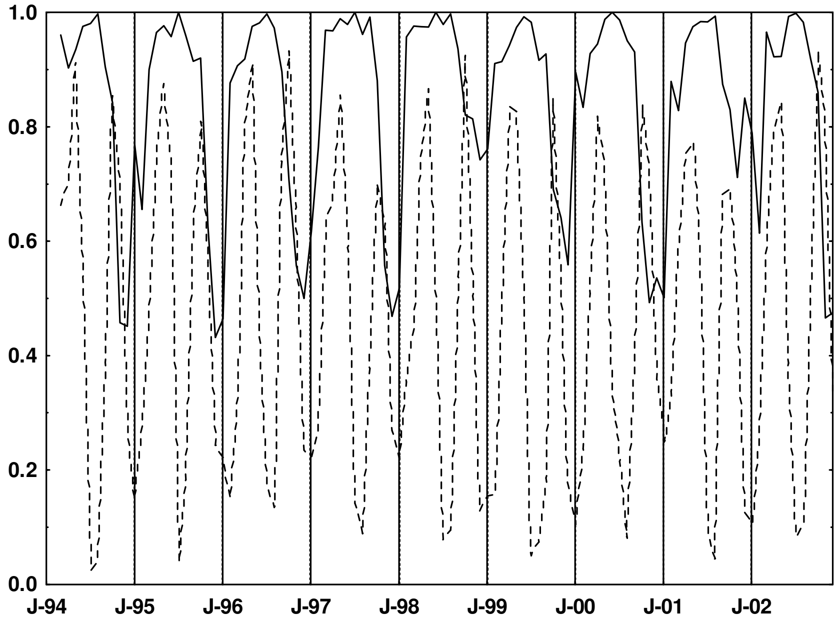

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}^{\ \alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\ \beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}^{\ \gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\ \delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	ε_i^2/N
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	1x10^{-5} day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R(1)*, Brigolin D.(1), Petrizzo A.(1), Zucchetta M.(2),

(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\dfrac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently “good” model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

Acknowledgements

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

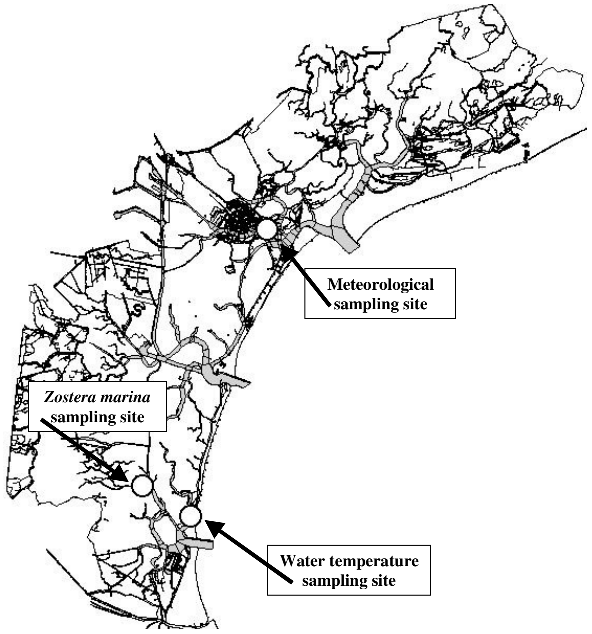

Figure 1. Data sampling sites

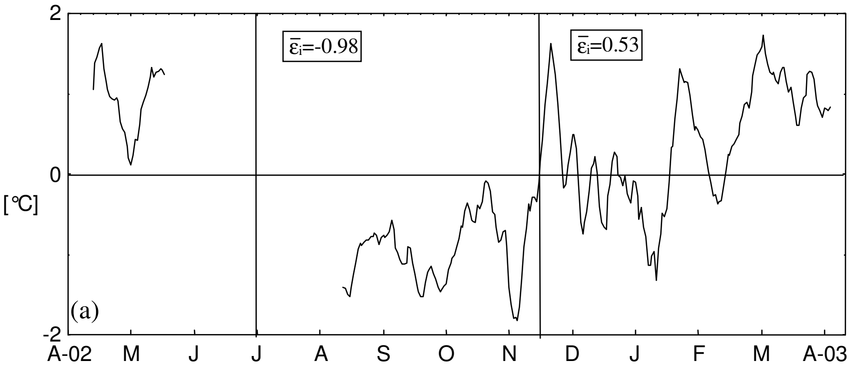

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

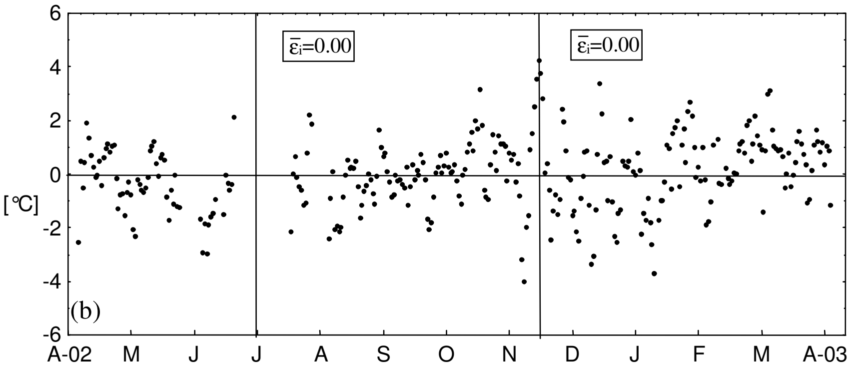

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

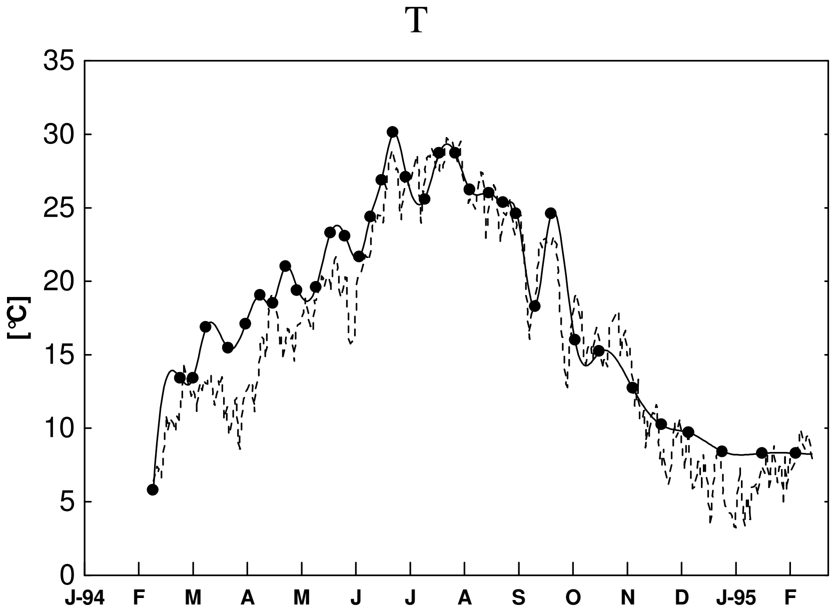

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

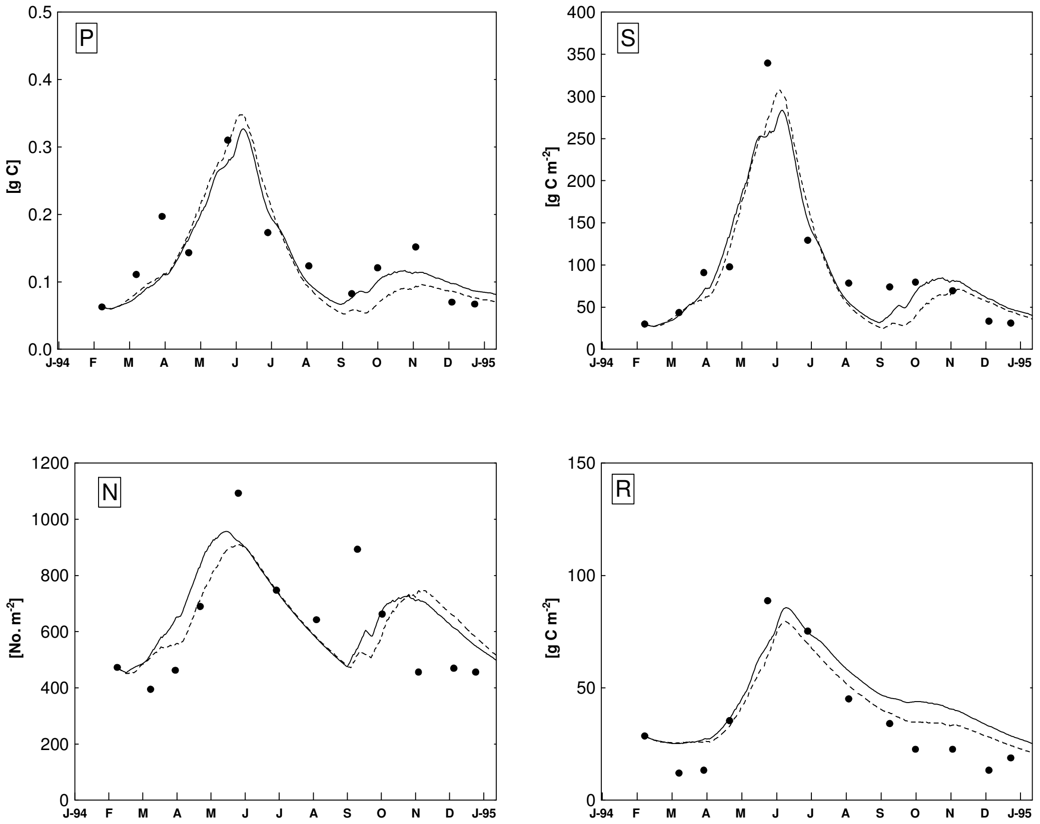

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

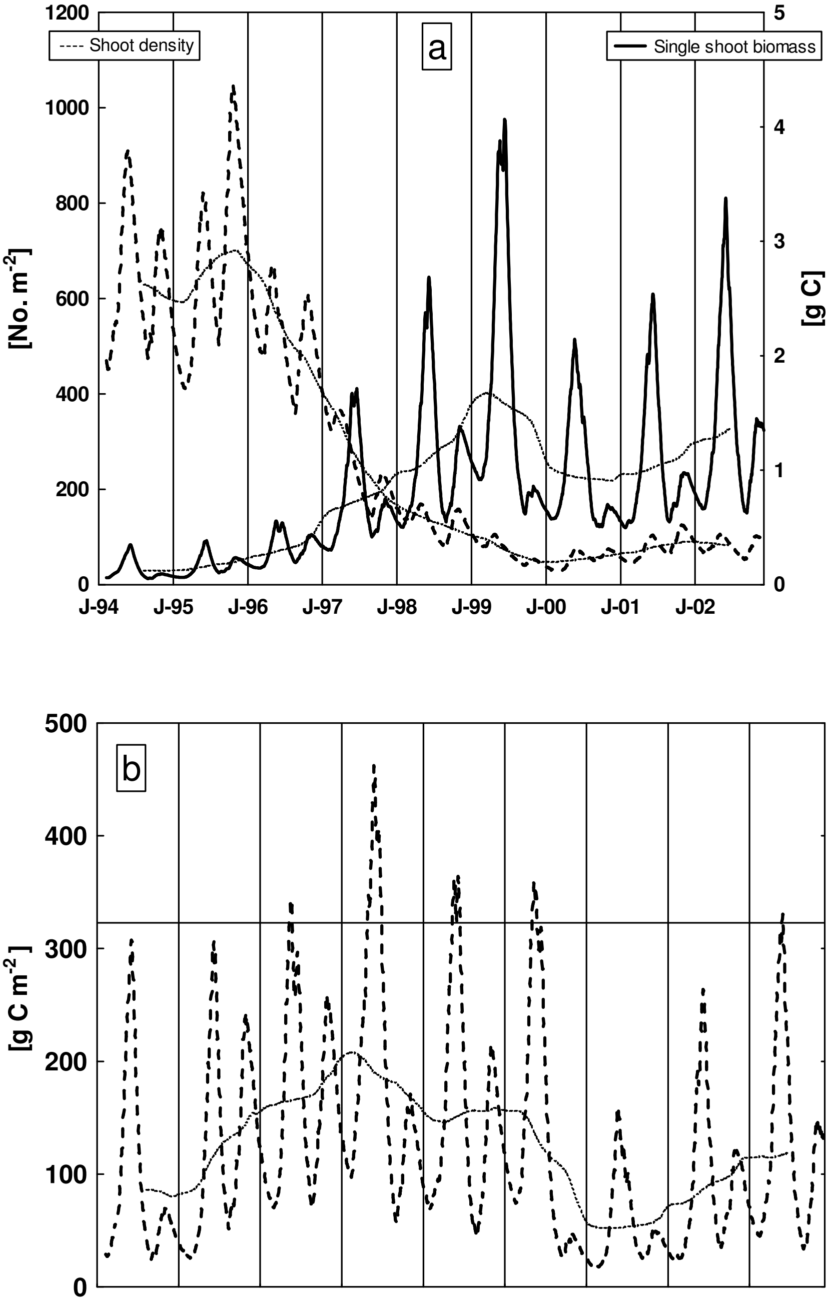

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

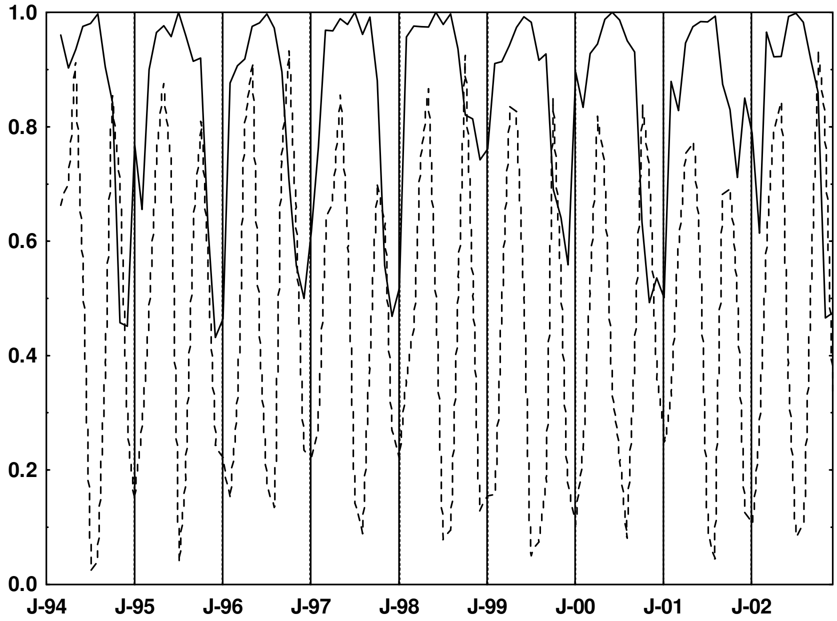

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}{}^{\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}{}^{\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}{}^{\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}{}^{\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec\,(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	ε_i^2/N
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1x10^{-5}$ day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R[(1)]*, Brigolin D.[(1)], Petrizzo A.[(1)], Zucchetta M.[(2)],

[(1)]Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
[(2)]Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \tag{3}$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently “good” model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. ‘Birthday effect’ on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

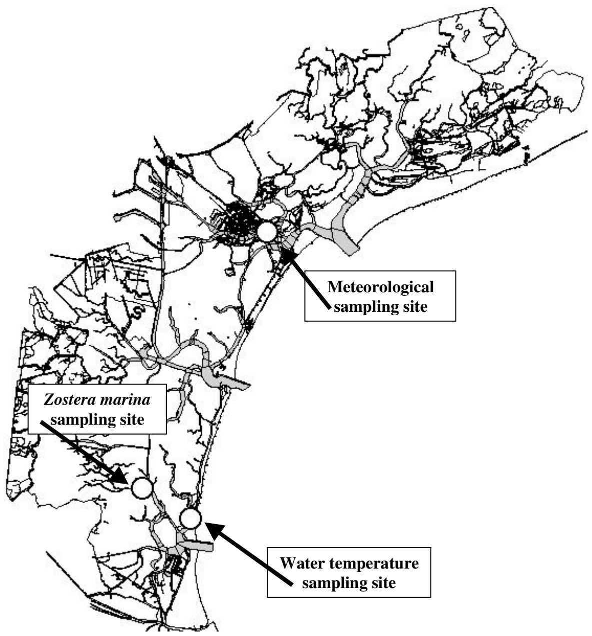

Figure 1. Data sampling sites

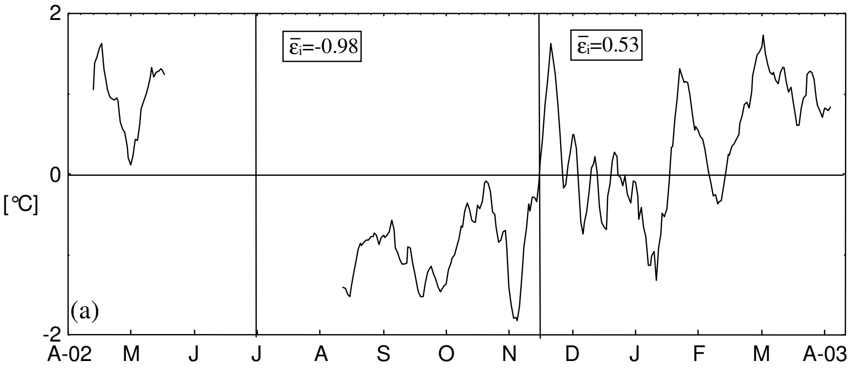

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

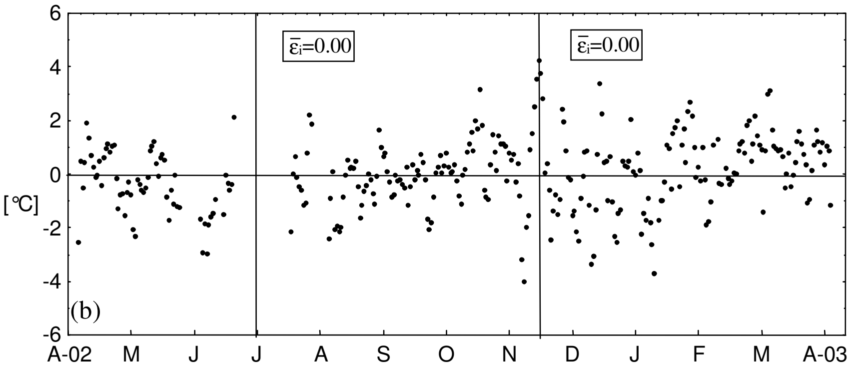

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

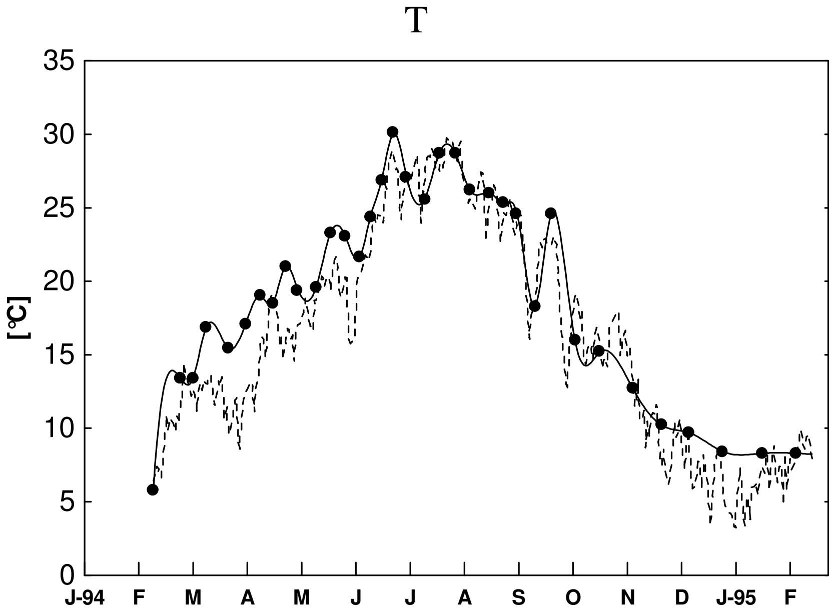

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

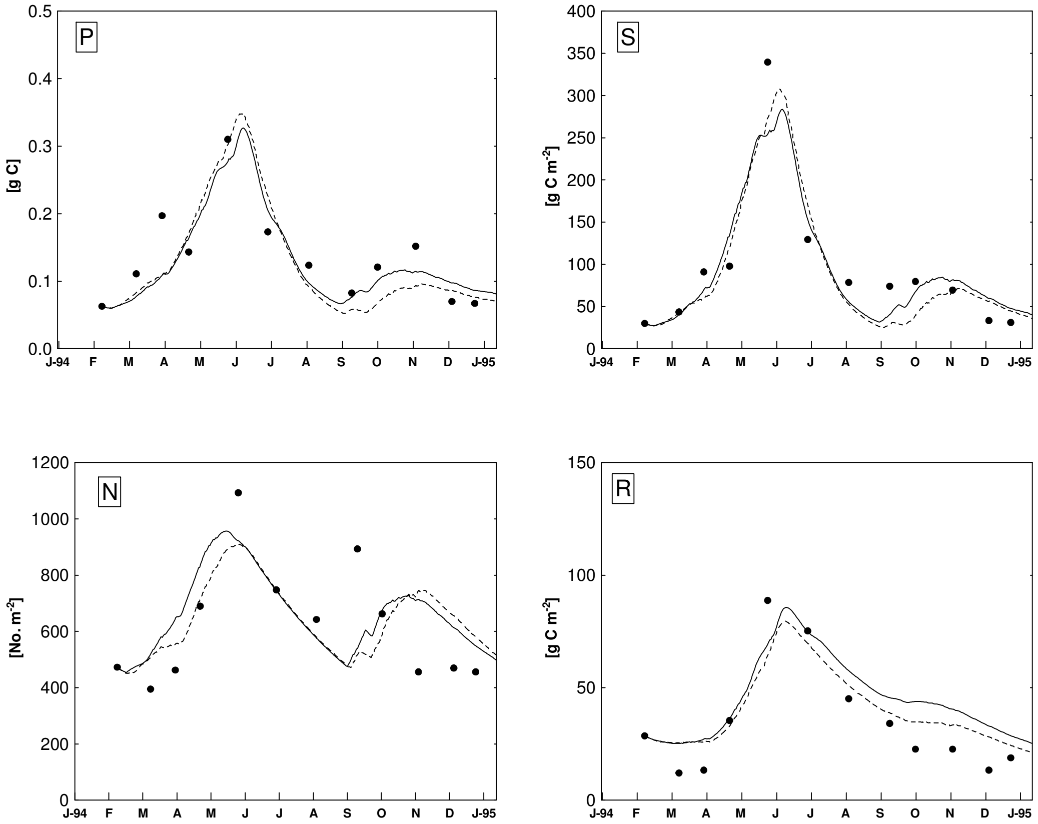

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

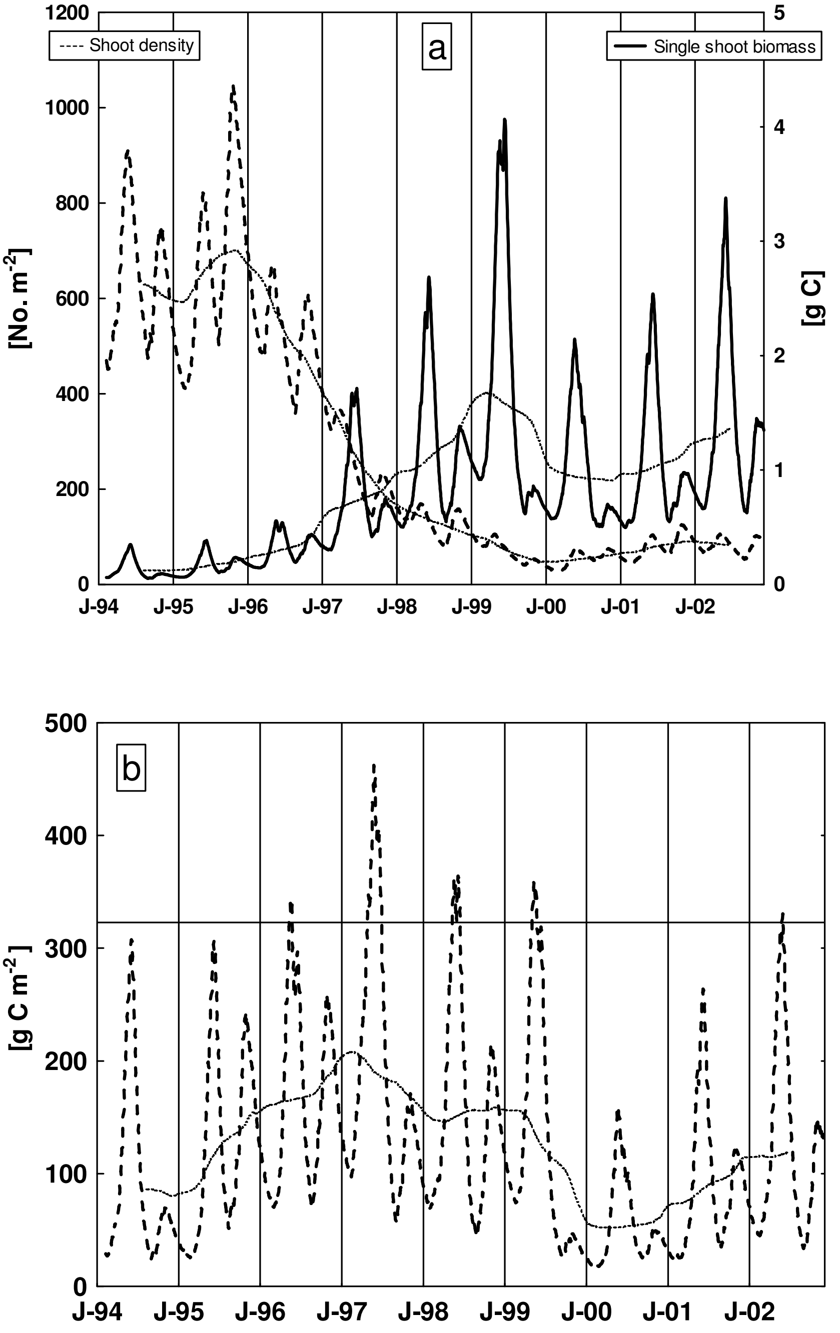

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

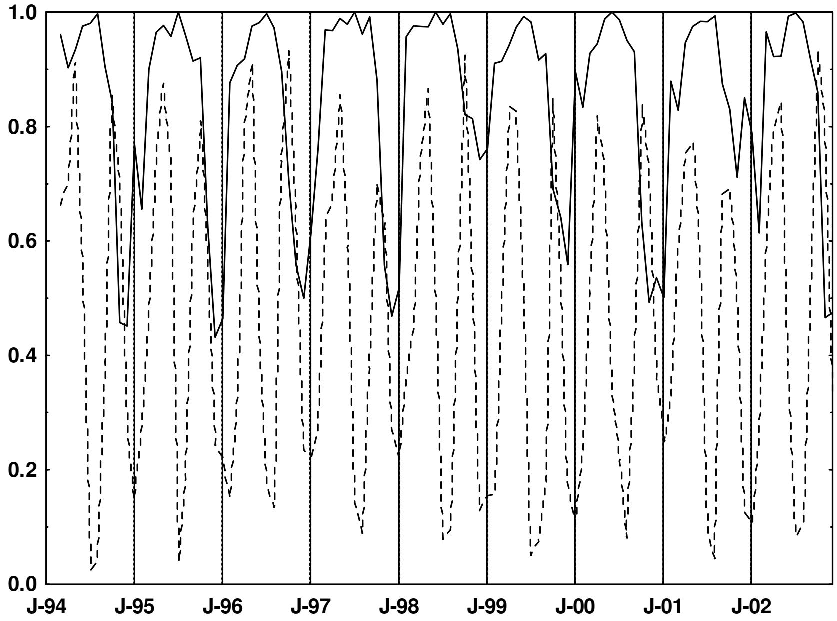

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}^{\ \alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\ \beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}^{\ \gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\ \delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	$\varepsilon_i^{\,2}/N$
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	$0.043\ \mathrm{day}^{-1}$	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	$0.028\ \mathrm{day}^{-1}$	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	$7.2\ 10^{-3}\ \mathrm{day}^{-1}$	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	$0.018\ \mathrm{day}^{-1}$	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	$0.009\ \mathrm{day}^{-1}$	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	$50\ \mathrm{g\ C\ m}^{-2}$	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	$0.0047\ \mathrm{g\ C\ m}^{-2}$	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	$25.5\ \mathrm{E\ m}^{-2}\ \mathrm{day}^{-1}$	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	$2.4\ \mathrm{E\ m}^{-2}\ \mathrm{day}^{-}$	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	$0.8\ \mathrm{m}^{-1}$	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	$0.01\ \mathrm{day}^{-1}$	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1\mathrm{x}10^{-5}\ \mathrm{day}^{-1}$	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	$0.0005\ \mathrm{day}^{-1}$	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	$0.00001\ \mathrm{day}^{-1}$	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R(1)*, Brigolin D.(1), Petrizzo A.(1), Zucchetta M.(2),

(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The *I* and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where *i* is the number of observations and *j* the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently “good” model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

Acknowledgements

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

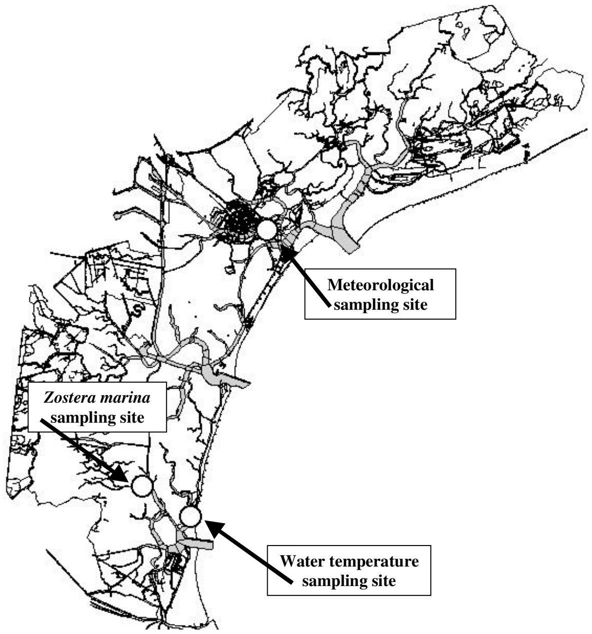

Figure 1. Data sampling sites

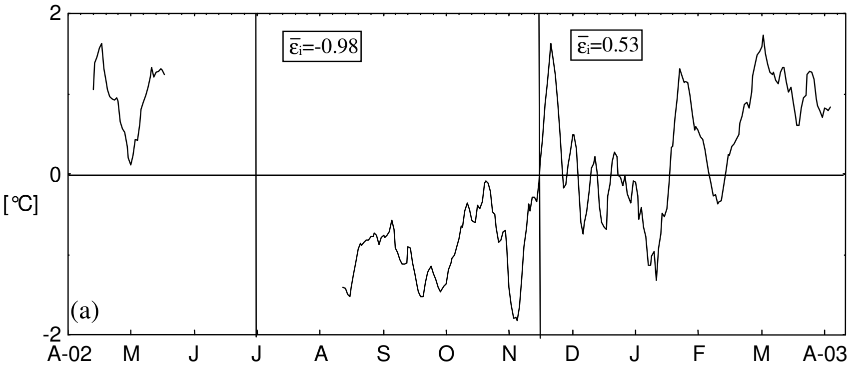

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

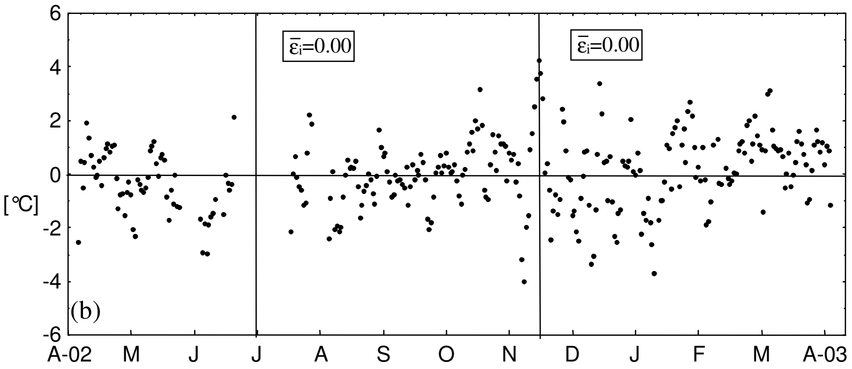

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

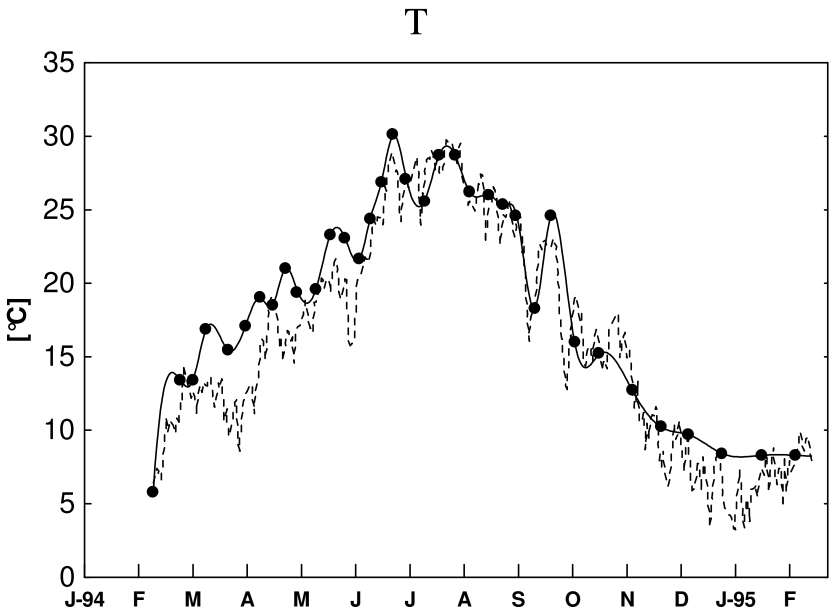

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

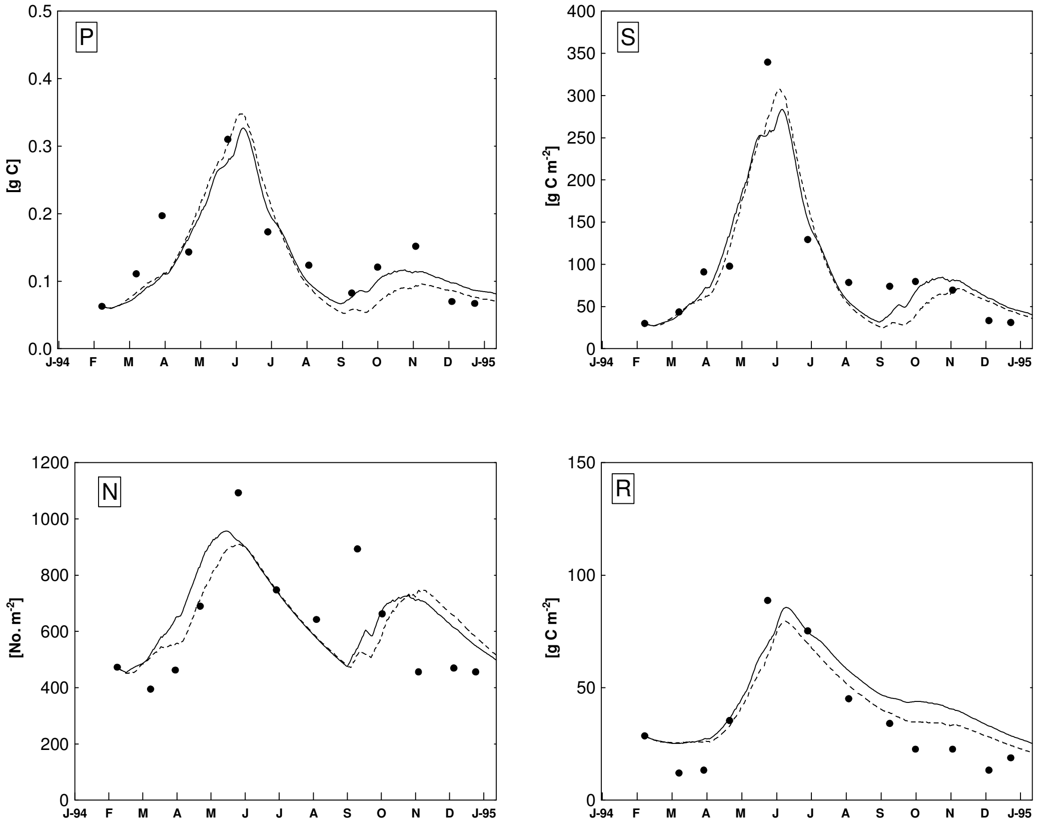

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

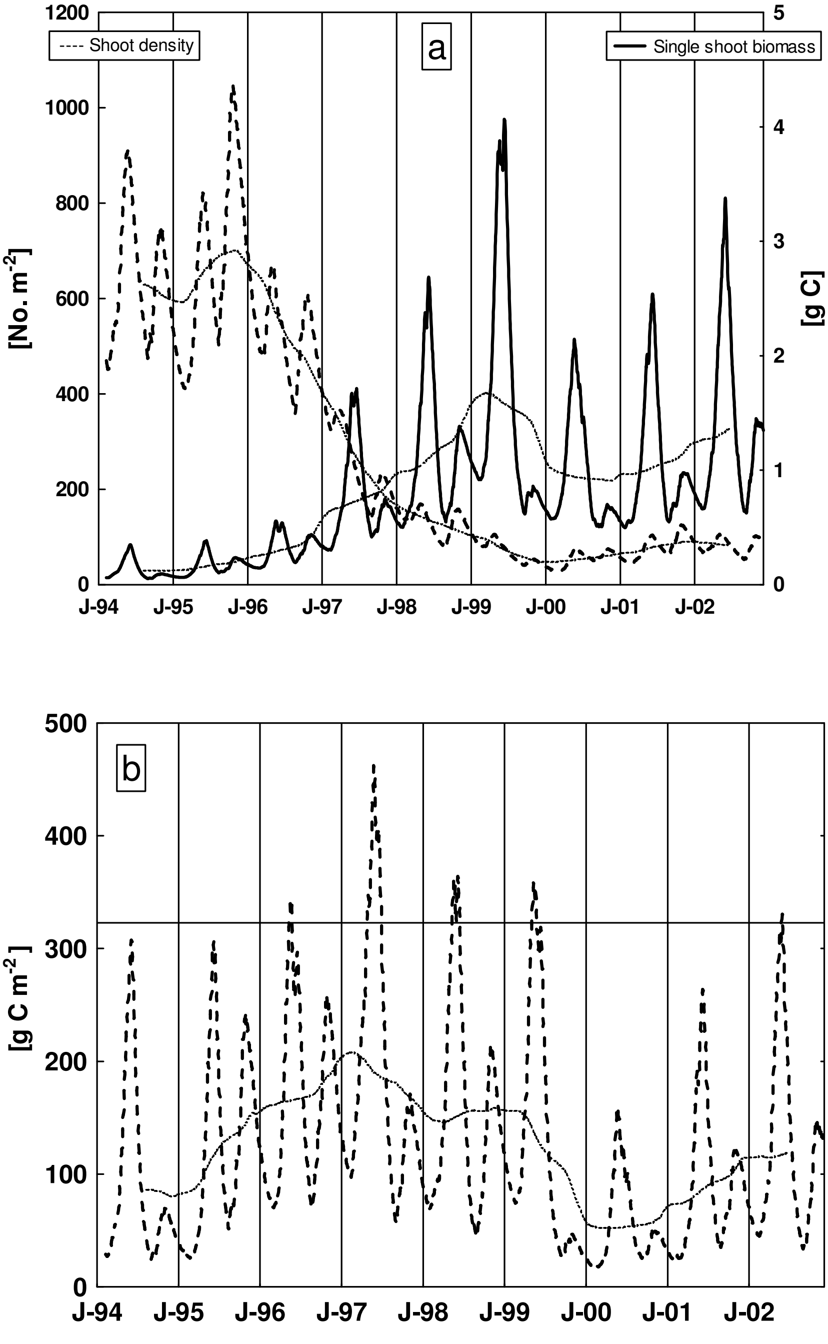

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

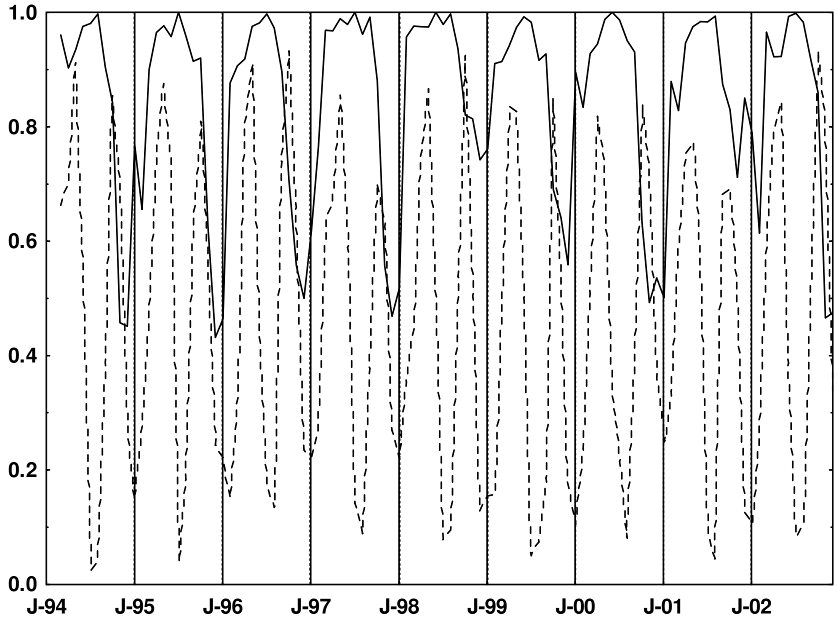

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}{}^{\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}{}^{\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}{}^{\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}{}^{\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	ε_i^2/N
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1x10^{-5}$ day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
stt_{phot}	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
stt_{prod}	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R(1)*, Brigolin D.(1), Petrizzo A.(1), Zucchetta M.(2),

(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \tag{3}$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently “good” model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

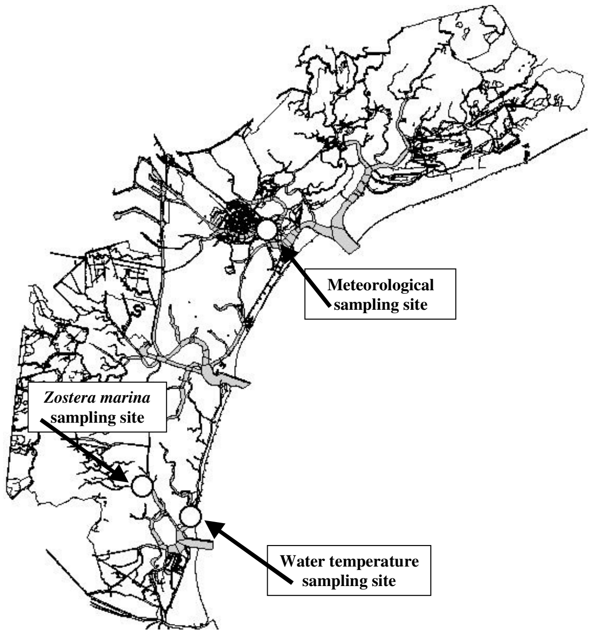

Figure 1. Data sampling sites

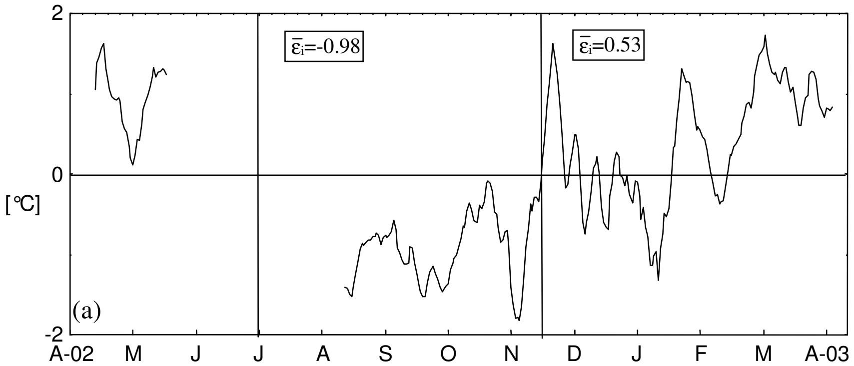

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

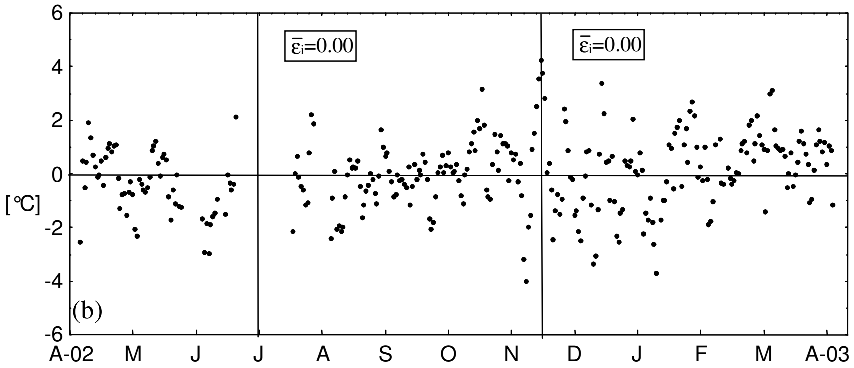

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

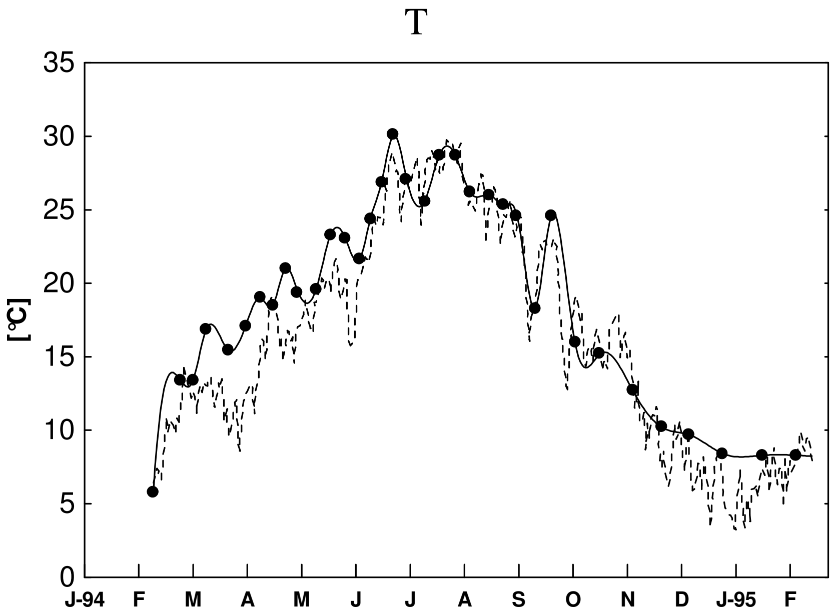

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

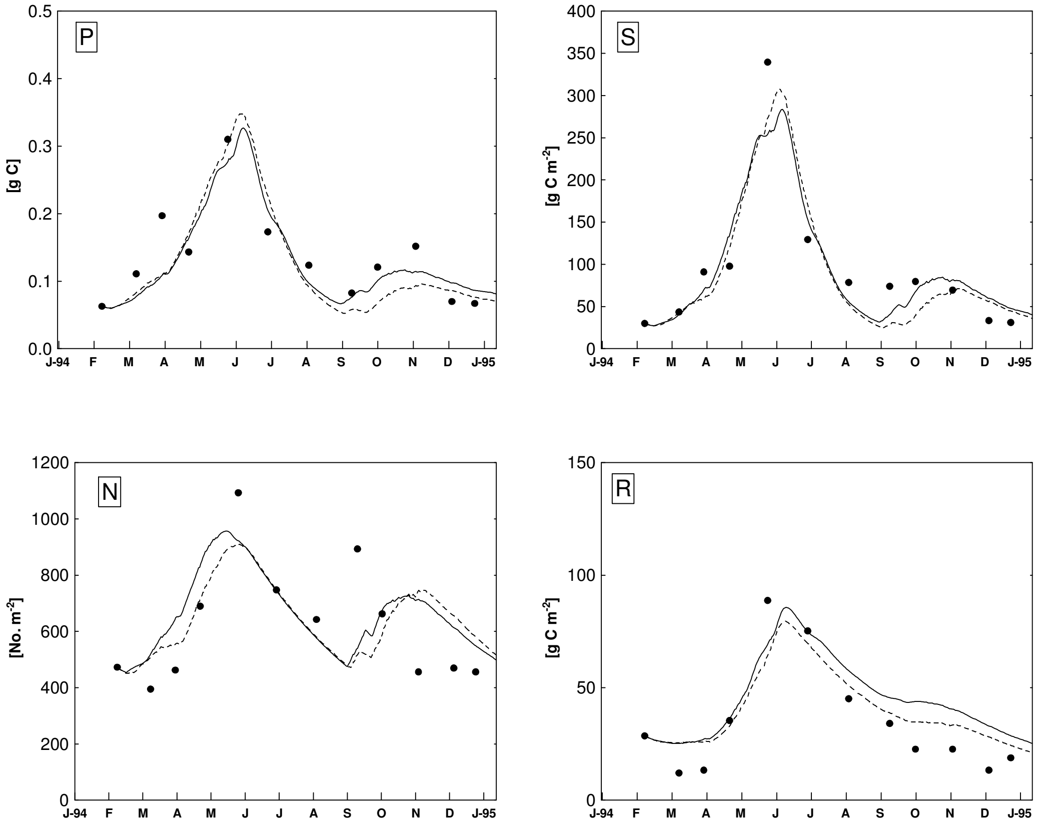

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

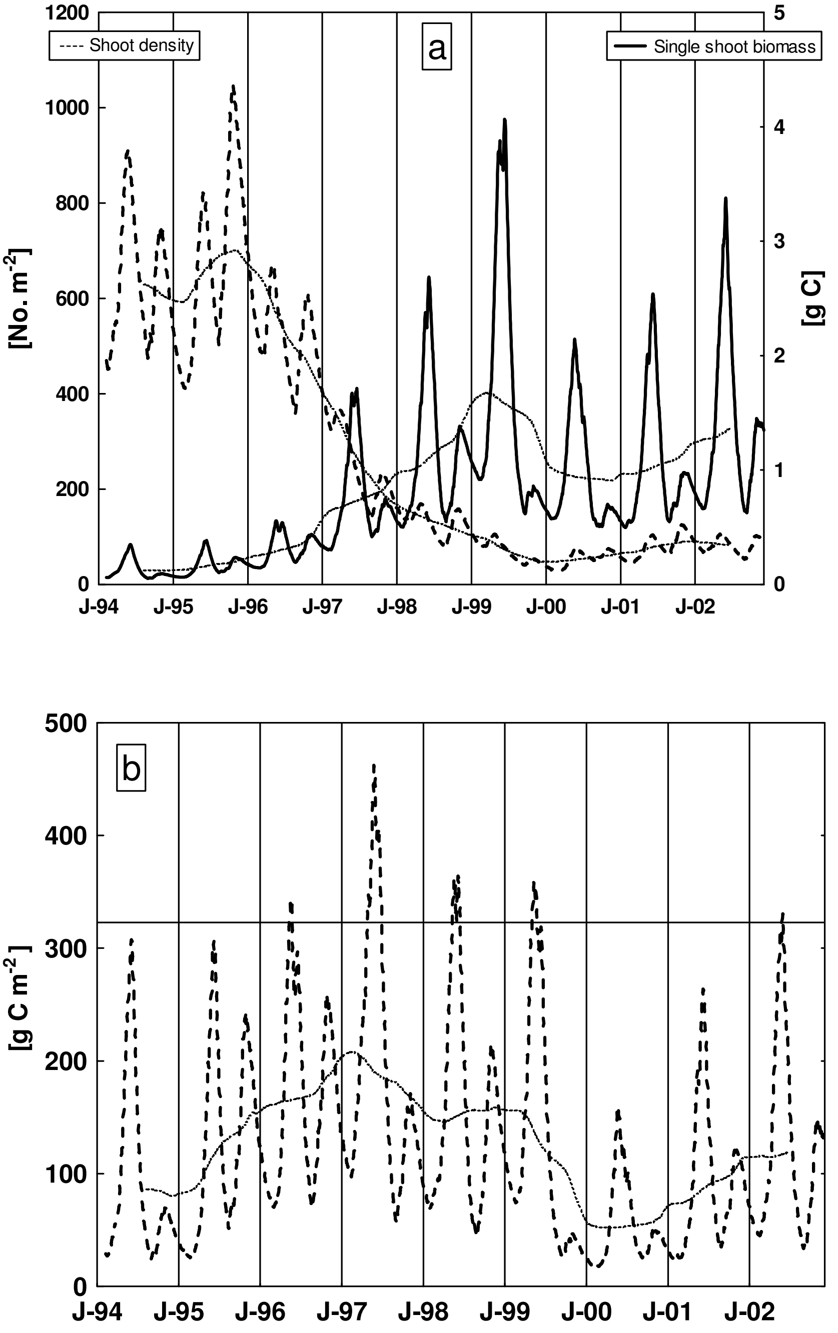

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

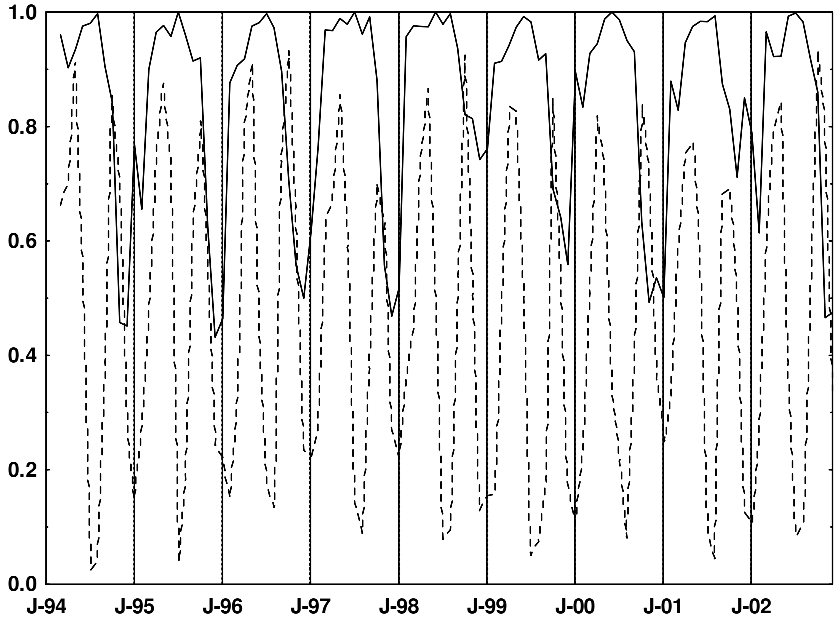

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}{}^{\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}{}^{\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}{}^{\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}{}^{\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	ε_i^2 / N
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	1×10^{-5} day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R$^{(1)}$*, Brigolin D.$^{(1)}$, Petrizzo A.$^{(1)}$, Zucchetta M.$^{(2)}$,

$^{(1)}$Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
$^{(2)}$Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The *I* and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\dfrac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \tag{3}$$

where *i* is the number of observations and *j* the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently "good" model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

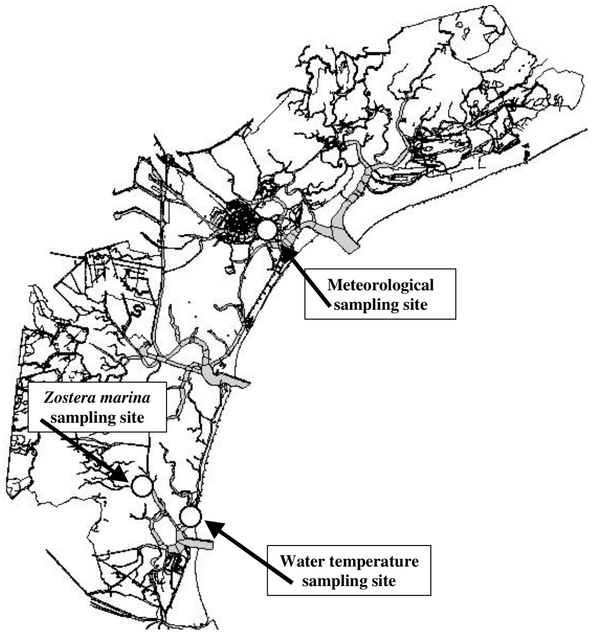

Figure 1. Data sampling sites

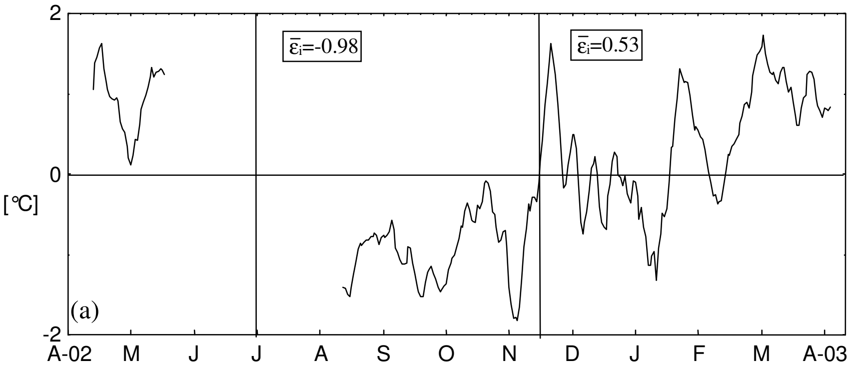

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

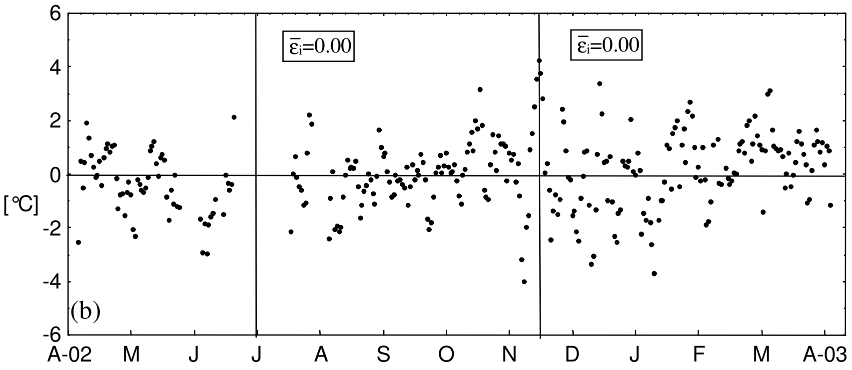

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

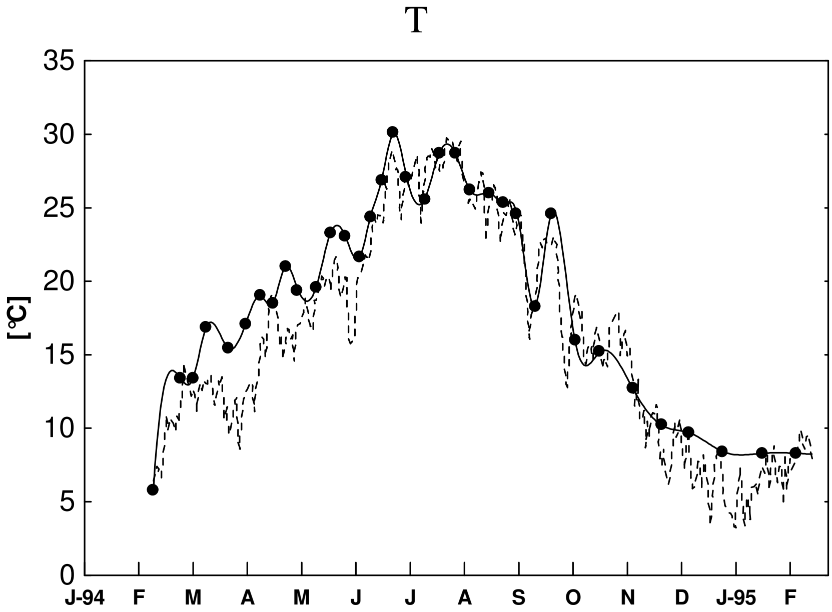

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

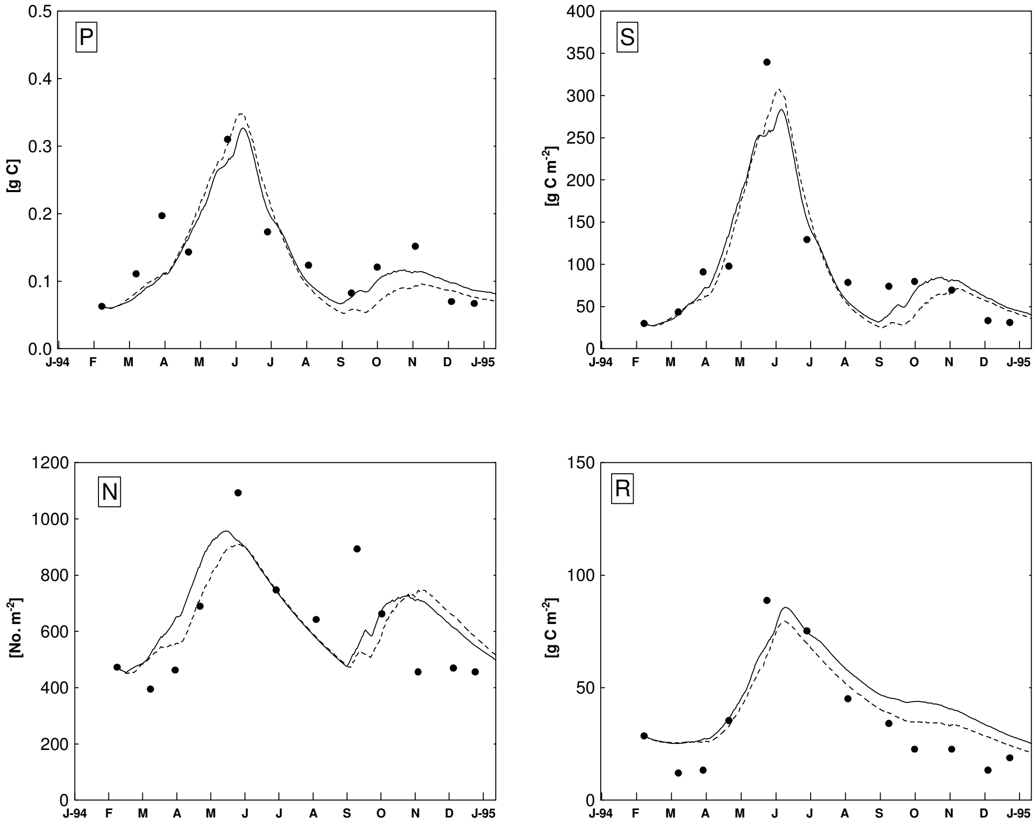

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

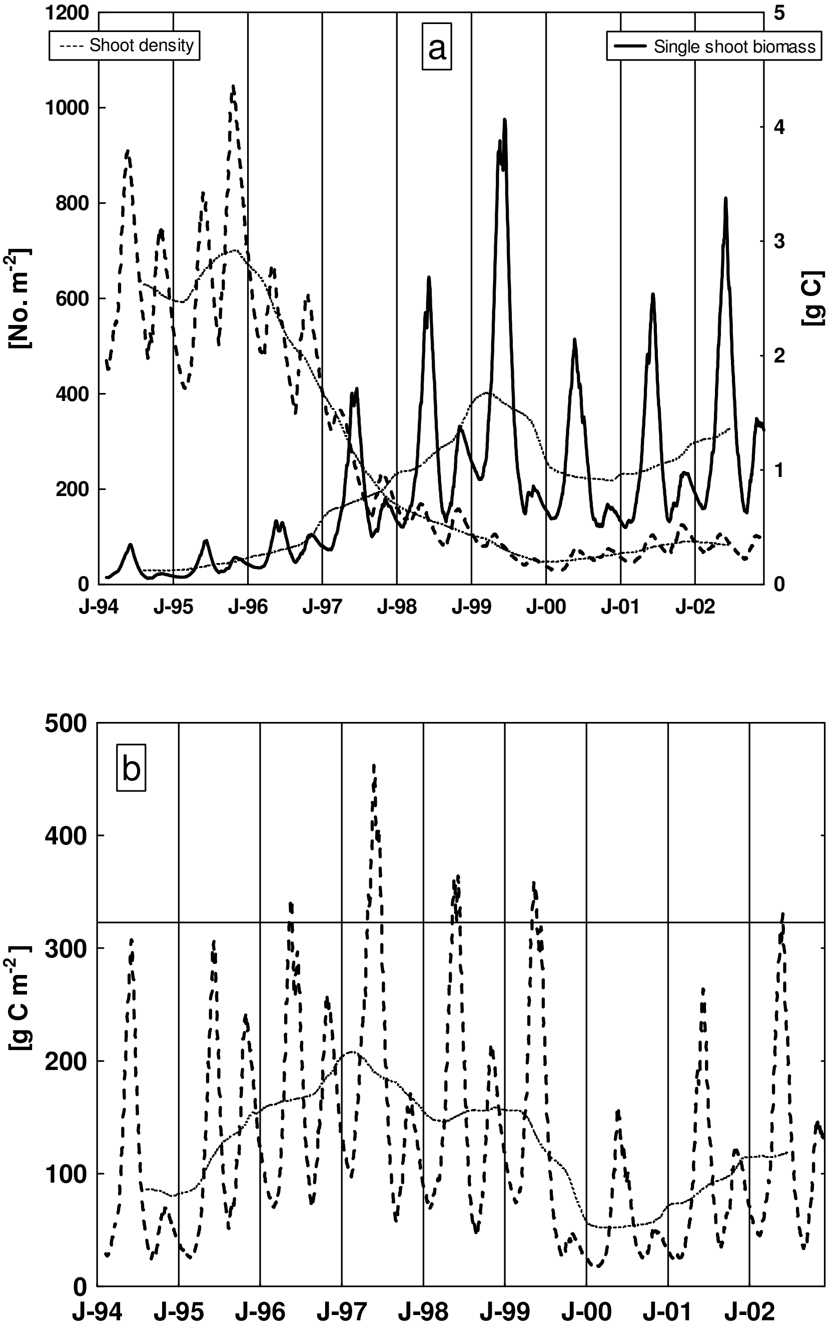

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

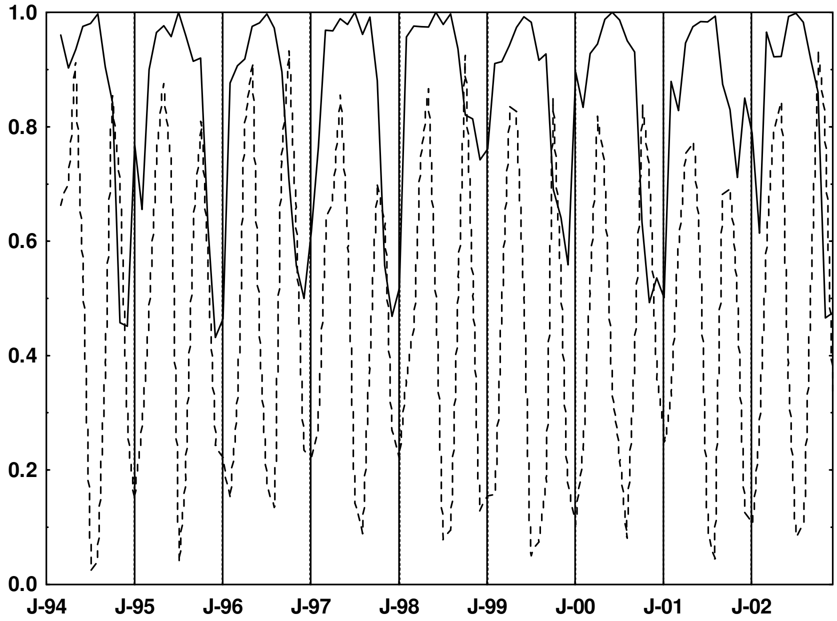

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}\left(T_w\right) = \begin{cases} k_{0\_phot}^{\;\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\;\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}}\right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}}\right)^{stt\_phot}$$

$$f_{\_prod}\left(T_w\right) = \begin{cases} k_{0\_prod}^{\;\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\;\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}}\right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}}\right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma}\right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec\ (T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	${\varepsilon_i}^2/N$
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	$0.043\ \text{day}^{-1}$	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	$0.028\ \text{day}^{-1}$	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	$7.2\ 10^{-3}\ \text{day}^{-1}$	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	$0.018\ \text{day}^{-1}$	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	$0.009\ \text{day}^{-1}$	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	$50\ \text{g C m}^{-2}$	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	$0.0047\ \text{g C m}^{-2}$	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	$25.5\ \text{E m}^{-2}\ \text{day}^{-1}$	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	$2.4\ \text{E m}^{-2}\ \text{day}^{-}$	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	$0.8\ \text{m}^{-1}$	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	$0.01\ \text{day}^{-1}$	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1\text{x}10^{-5}\ \text{day}^{-1}$	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	$0.0005\ \text{day}^{-1}$	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	$0.00001\ \text{day}^{-1}$	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R(1)*, Brigolin D.(1), Petrizzo A.(1), Zucchetta M.(2),

(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy

(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy

*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The *I* and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where *i* is the number of observations and *j* the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently “good” model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

Acknowledgements

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. ‘Birthday effect’ on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

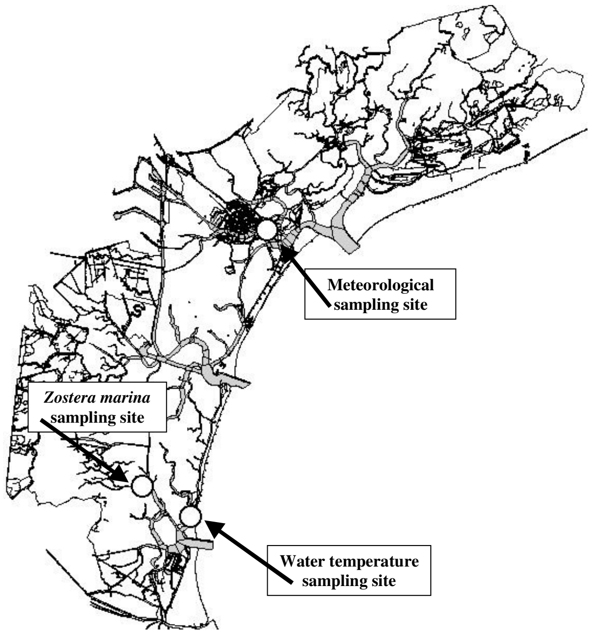

Figure 1. Data sampling sites

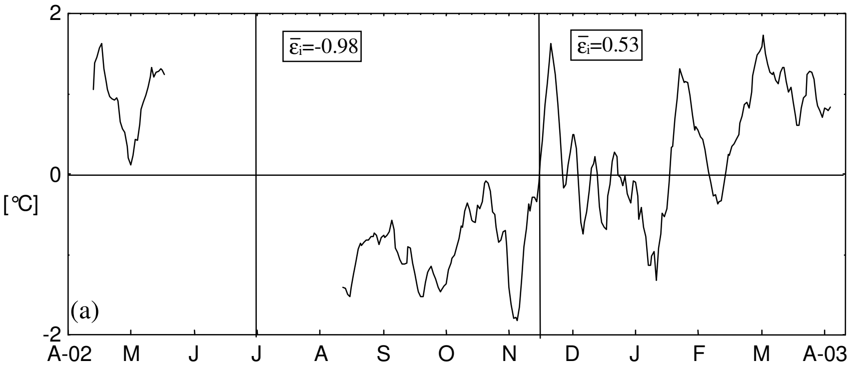

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

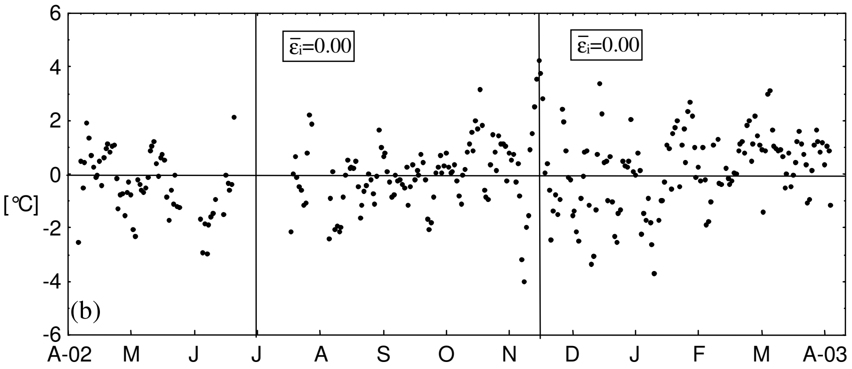

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

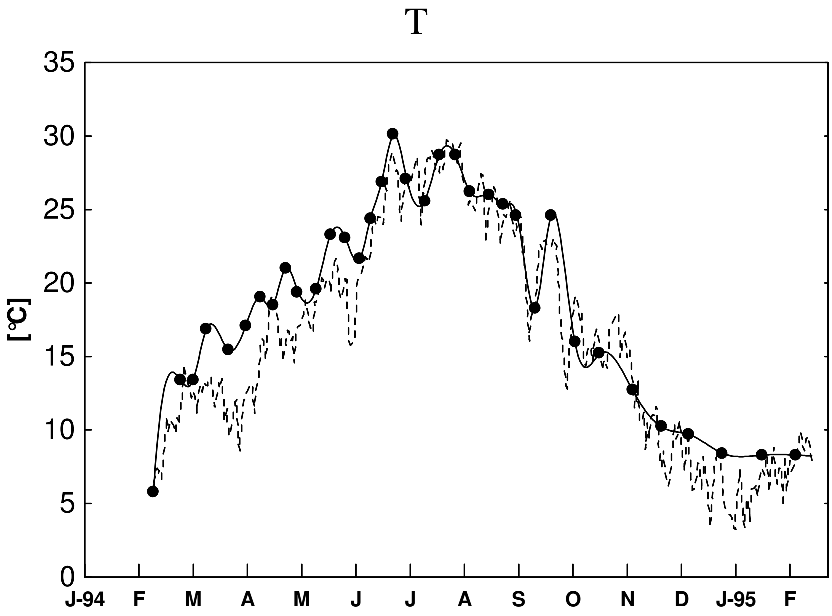

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

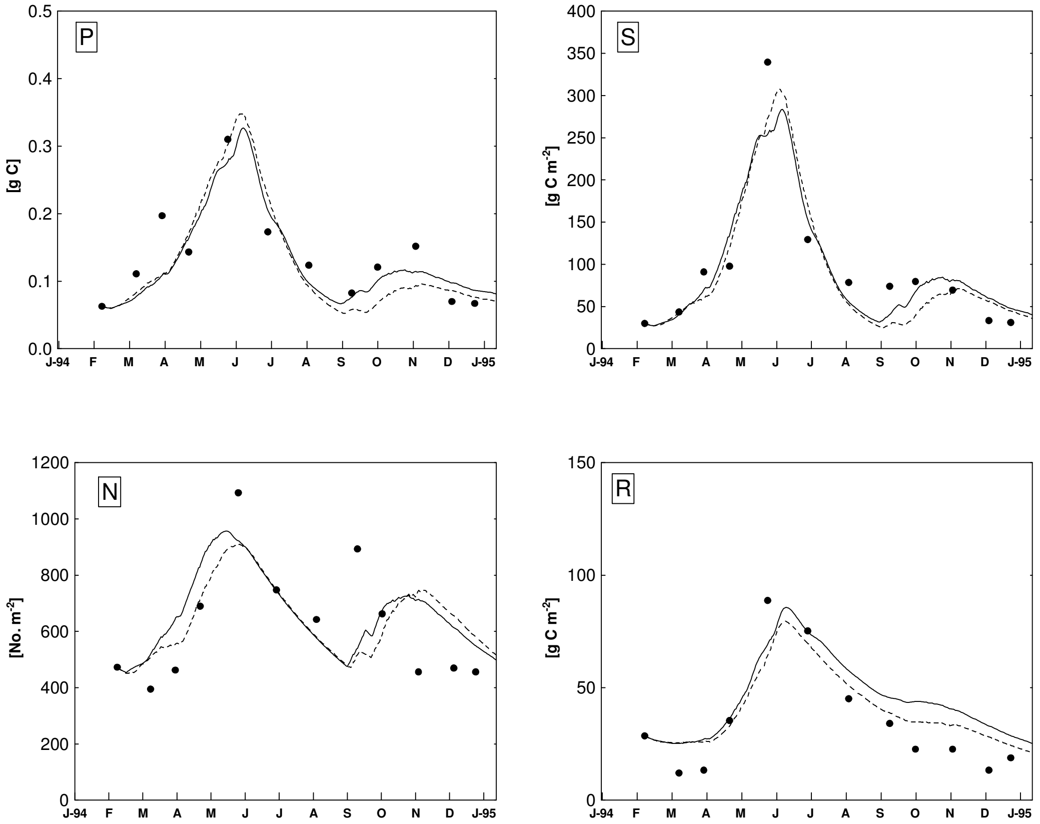

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

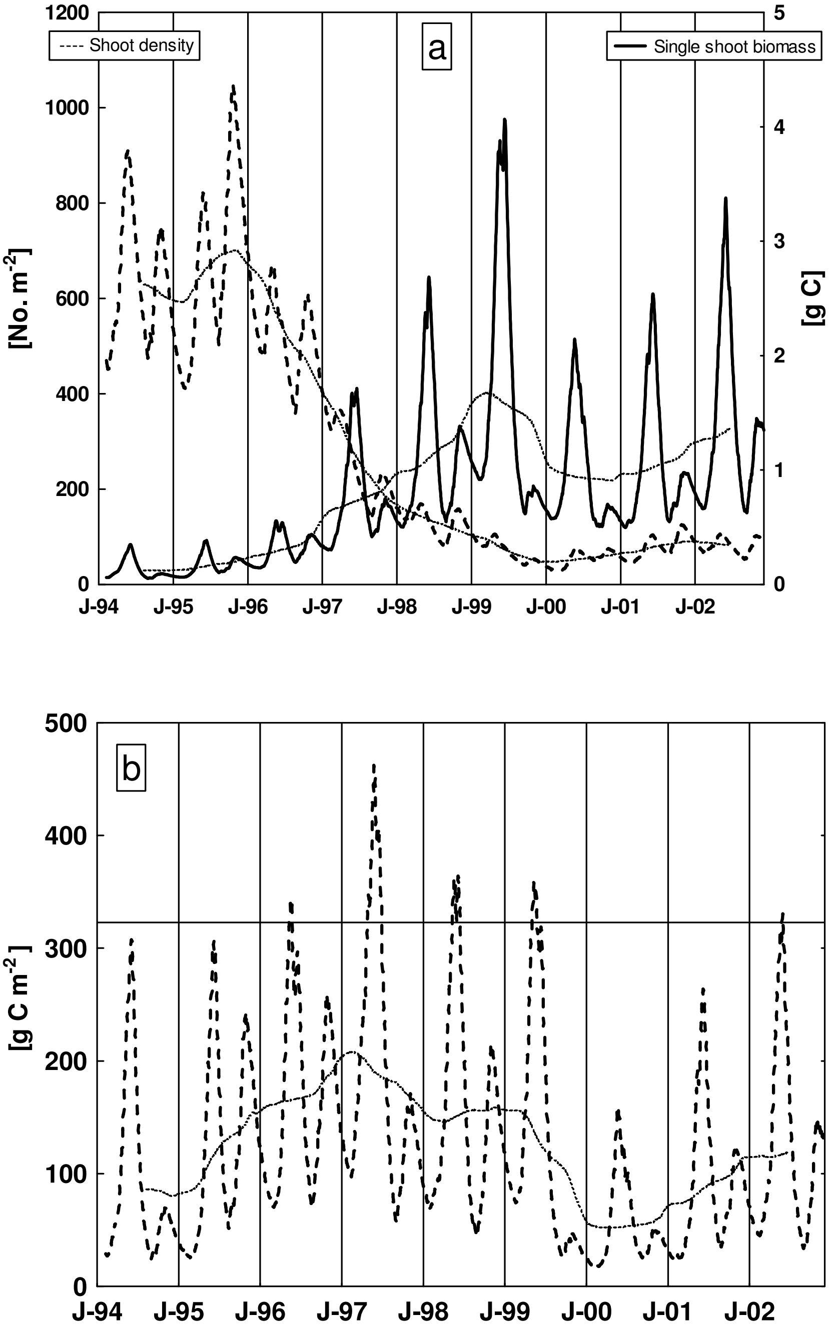

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

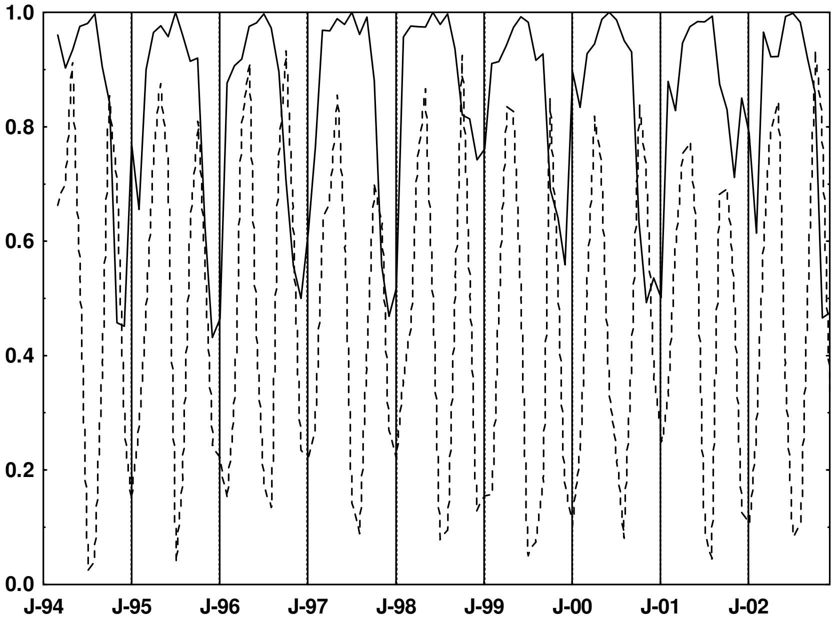

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}{}^{\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}{}^{\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}{}^{\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}{}^{\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	${\varepsilon_i}^2/N$
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	1x10^{-5} day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R[(1)]*, Brigolin D.[(1)], Petrizzo A.[(1)], Zucchetta M.[(2)],

[(1)]Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
[(2)]Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently “good” model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. ‘Birthday effect’ on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

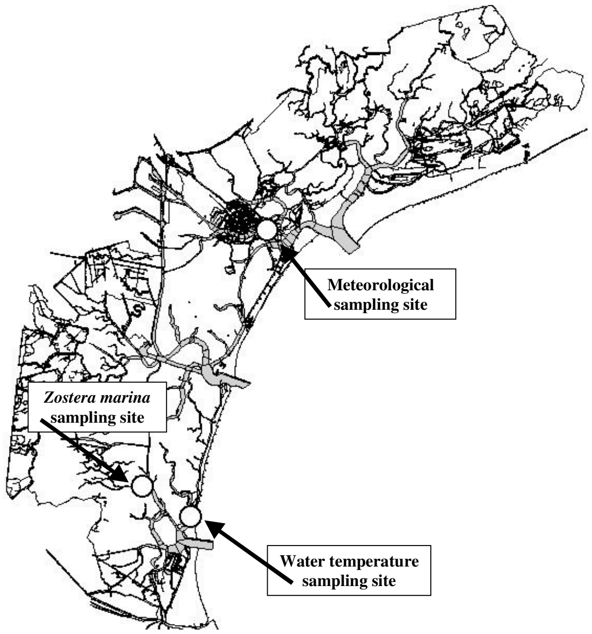

Figure 1. Data sampling sites

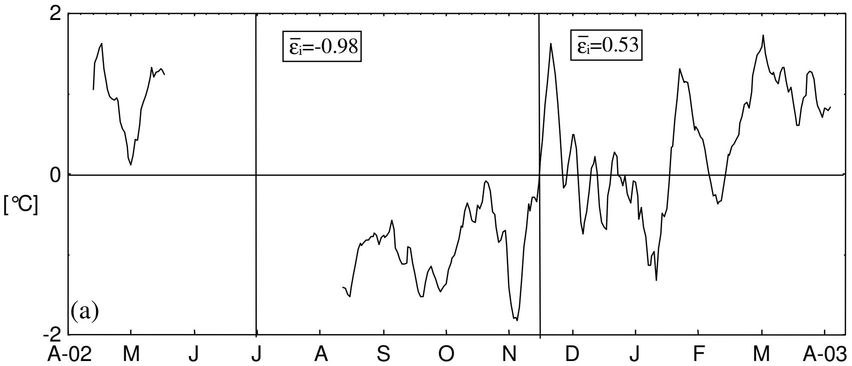

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

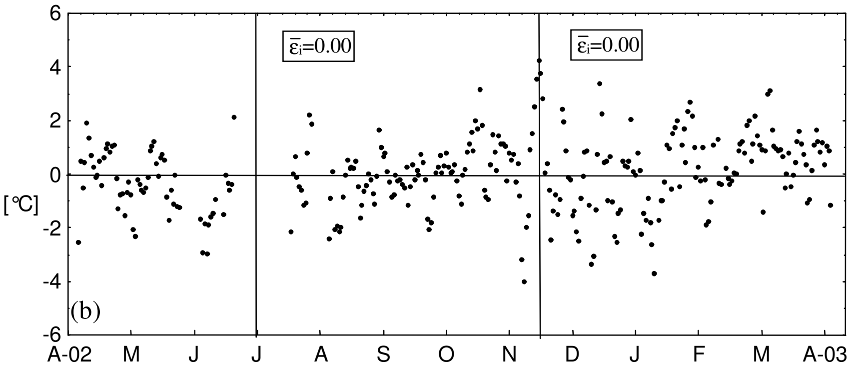

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

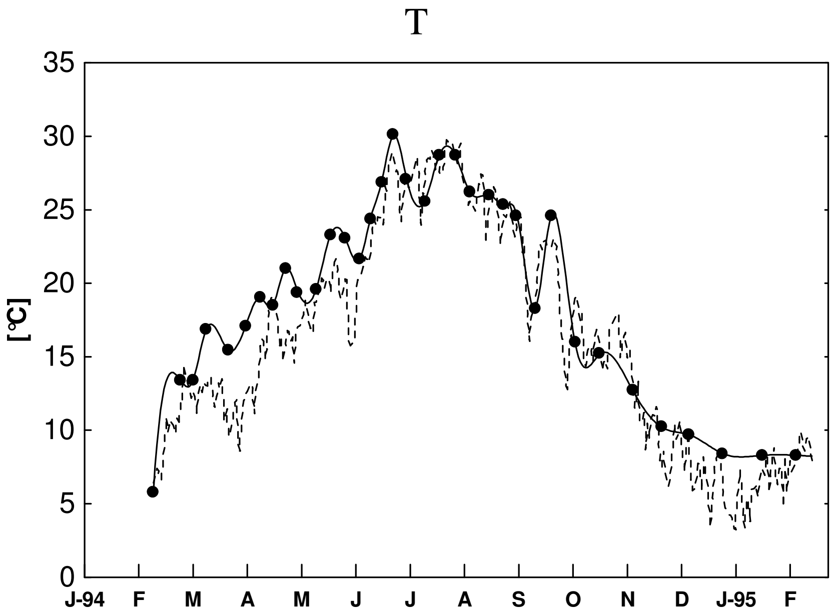

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

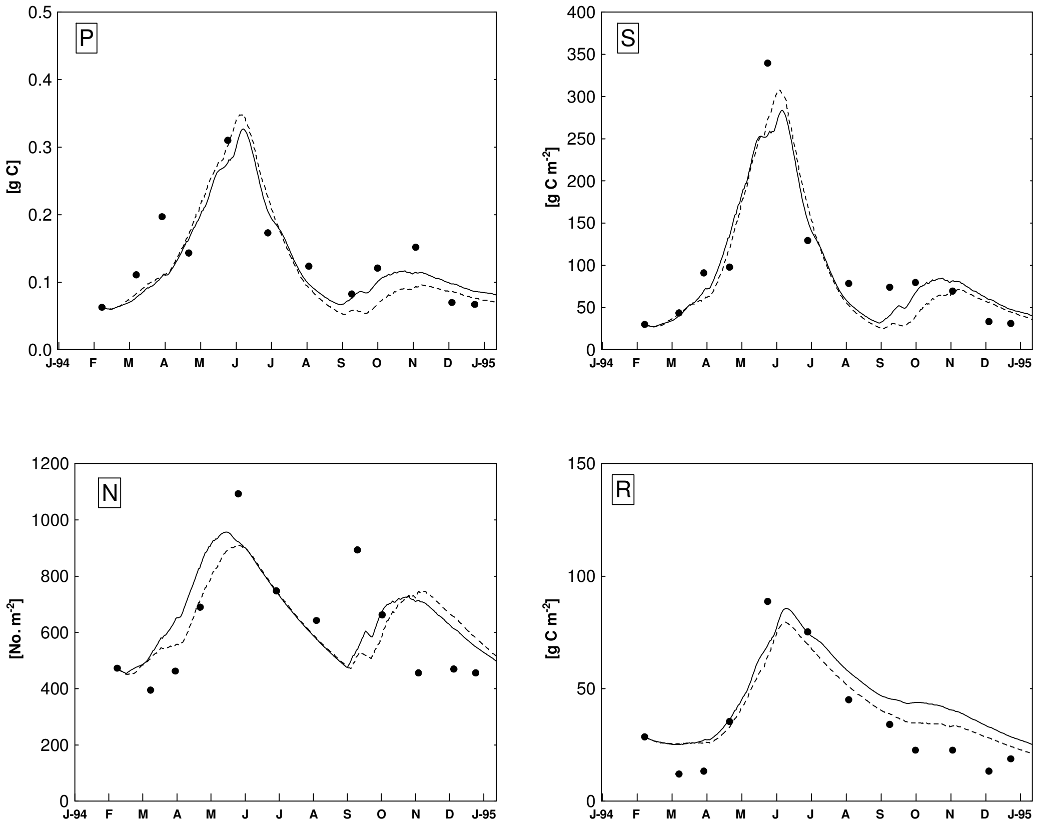

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

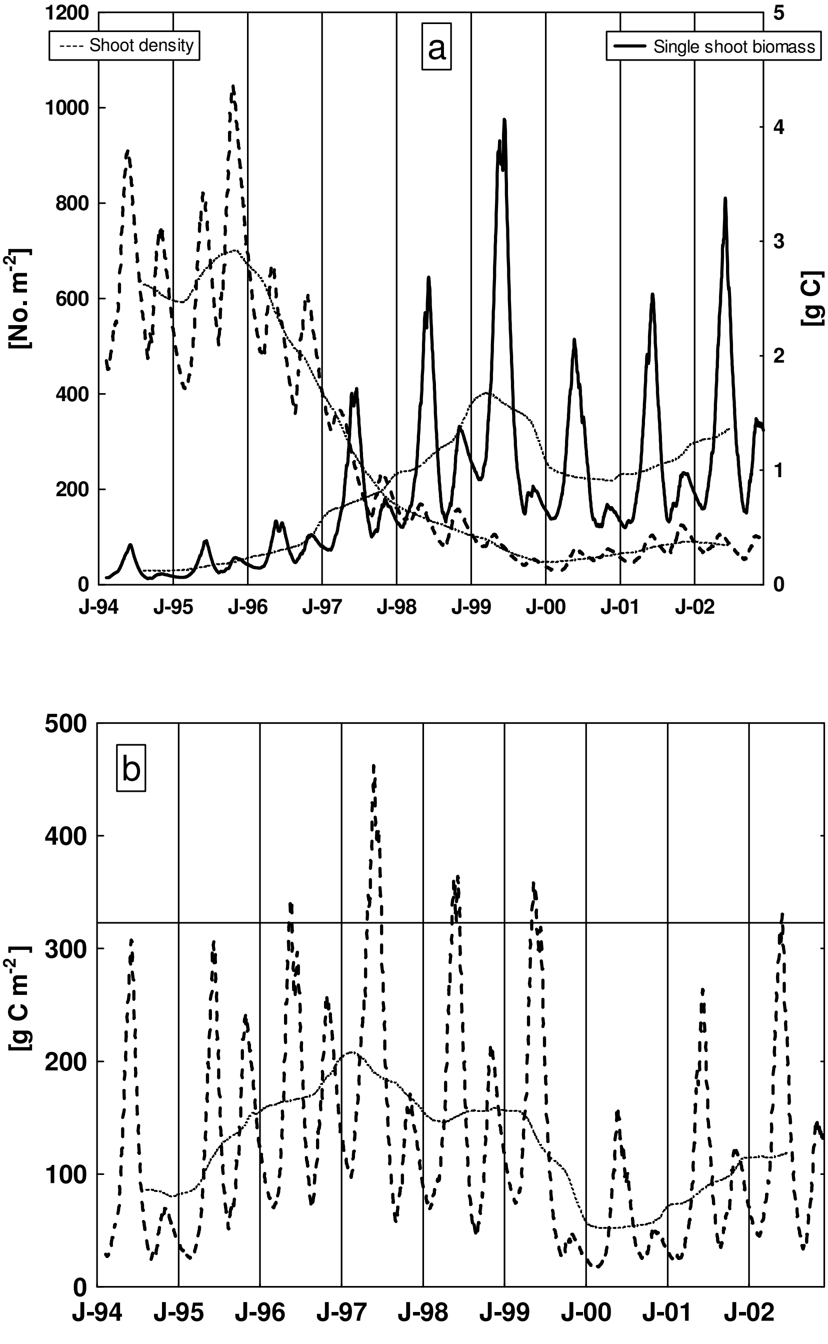

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

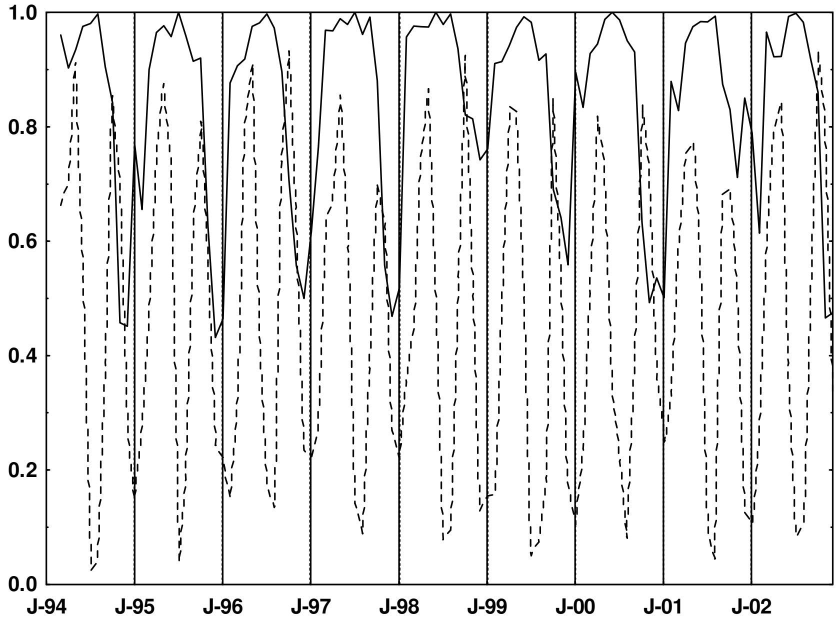

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}^{\ \alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\ \beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}^{\ \gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\ \delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	ε_i^2/N
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	$7.2\ 10^{-3}$ day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1x10^{-5}$ day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R[(1)]*, Brigolin D.[(1)], Petrizzo A.[(1)], Zucchetta M.[(2)],

[(1)]Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
[(2)]Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \tag{3}$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently "good" model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

Acknowledgements

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

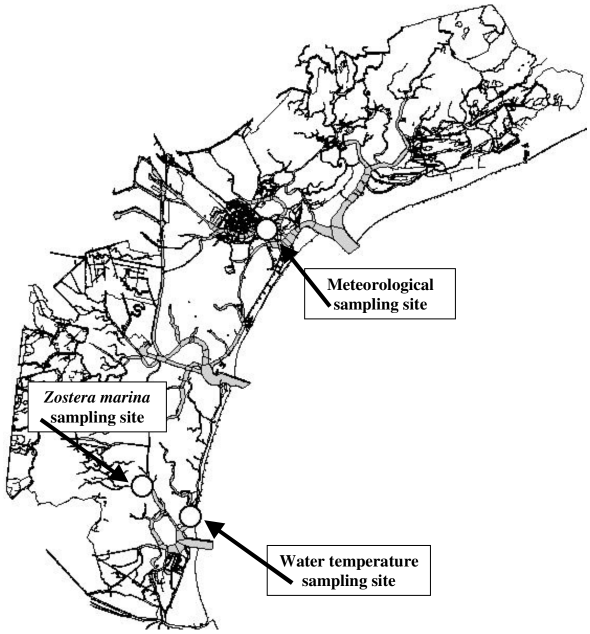

Figure 1. Data sampling sites

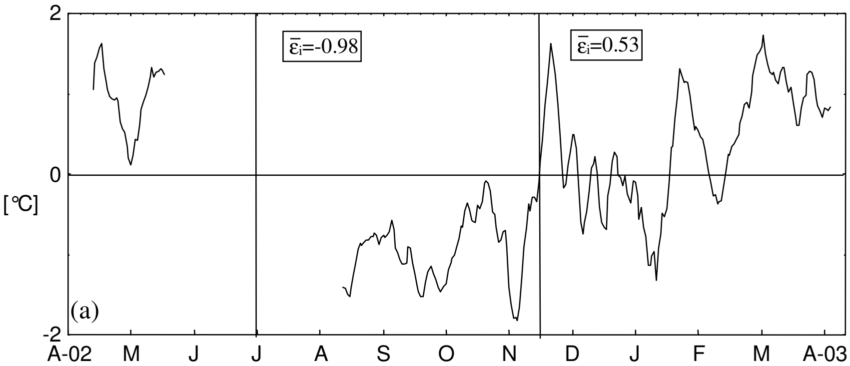

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

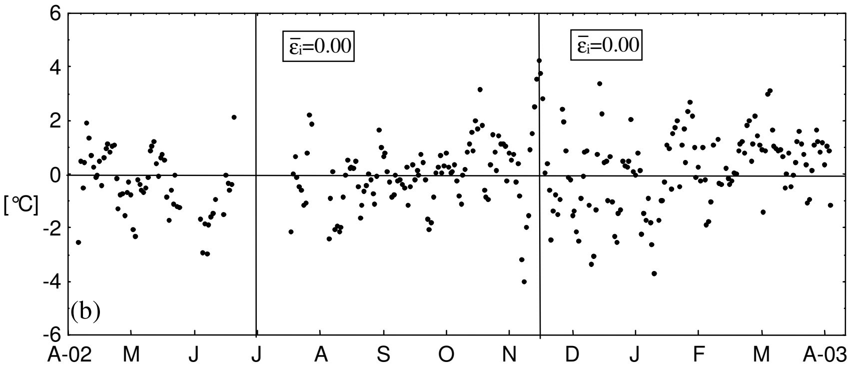

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

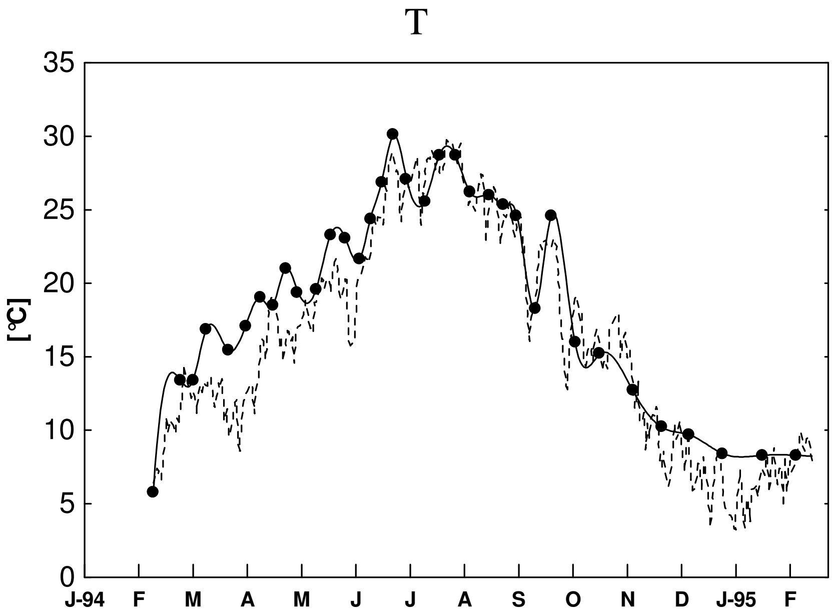

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

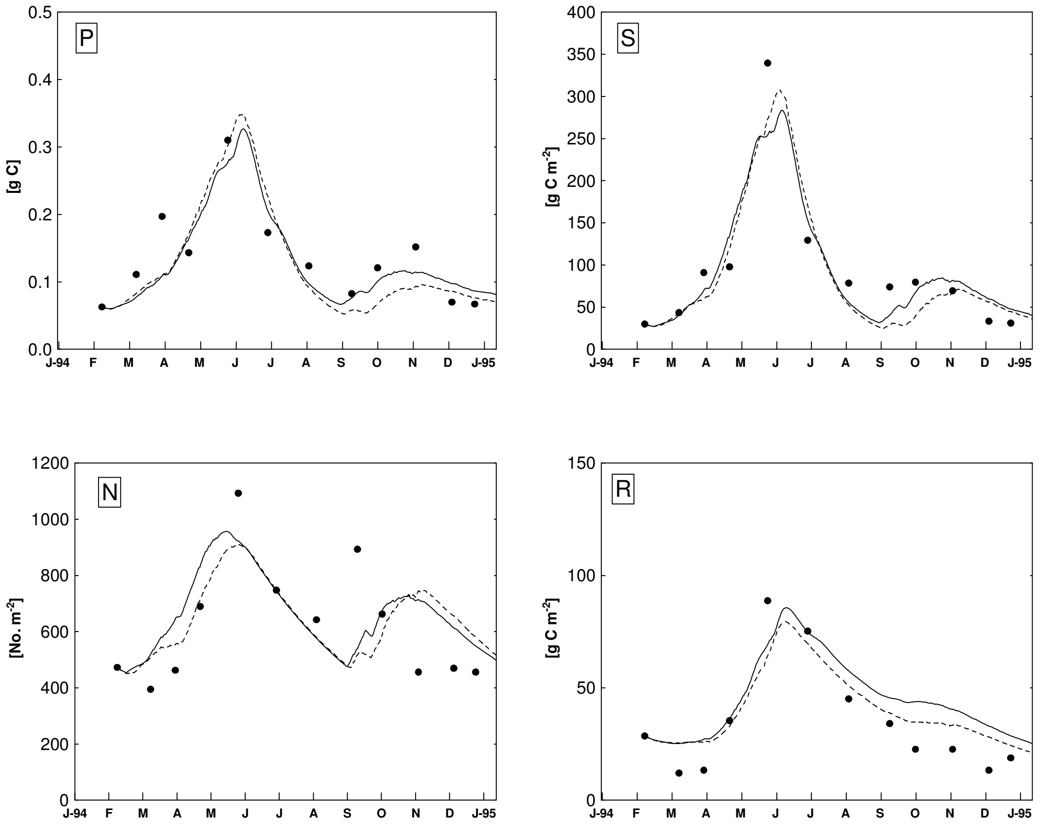

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

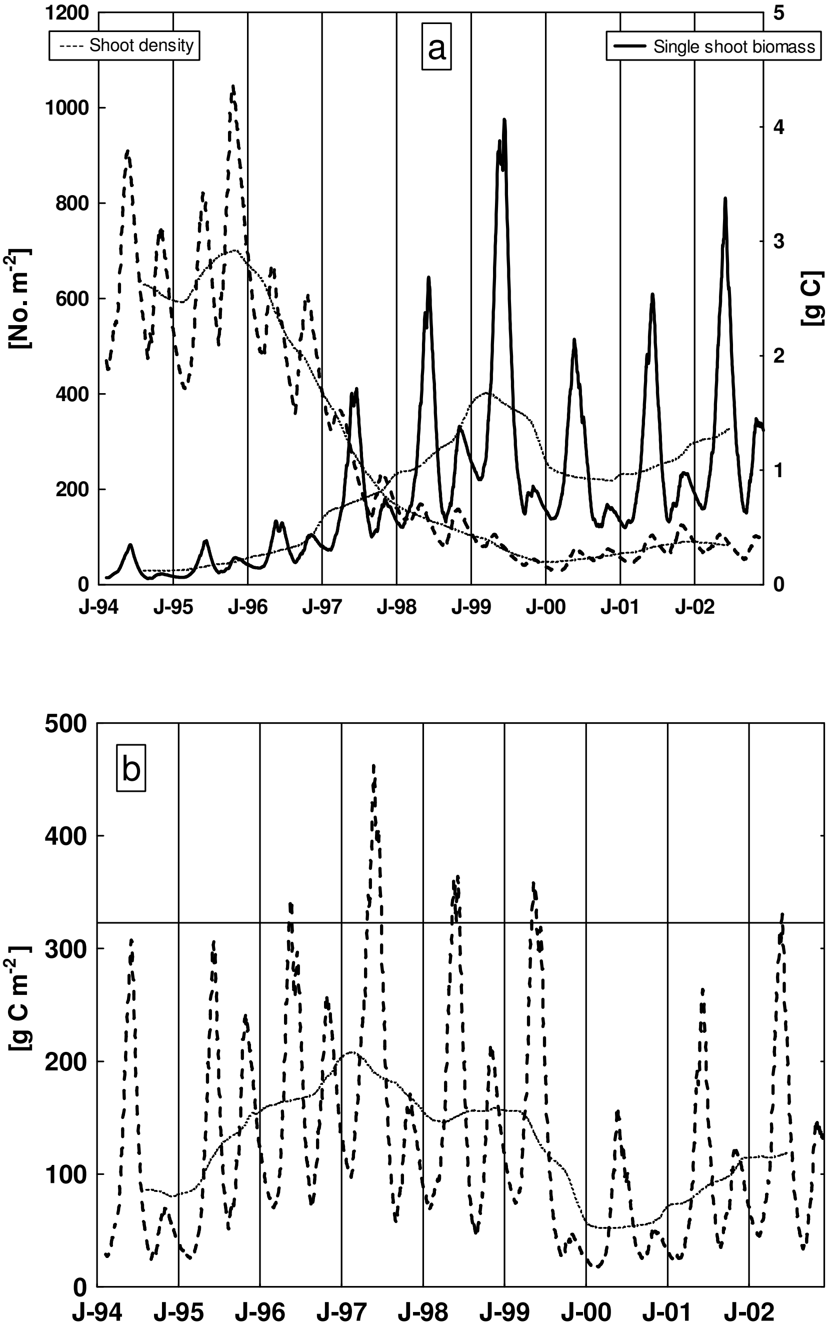

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

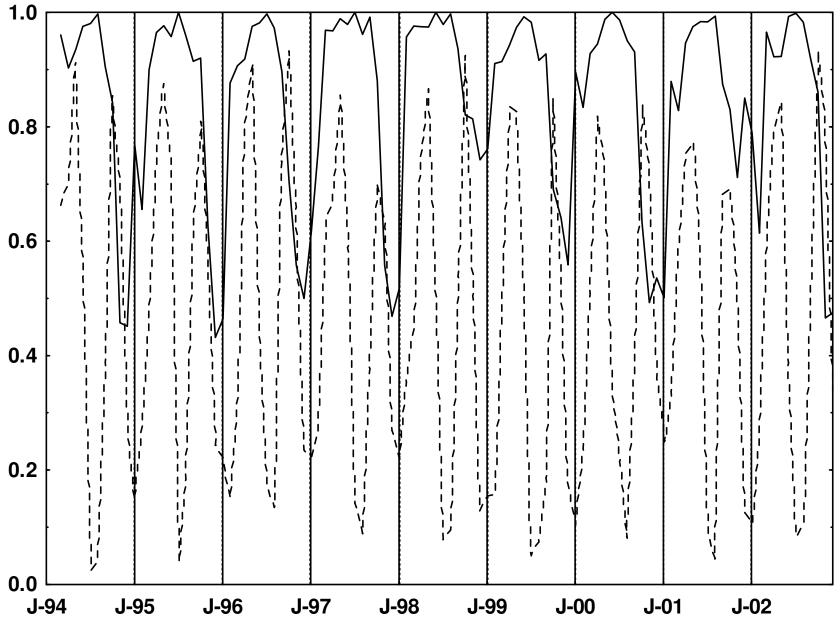

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}^{\ \alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\ \beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}^{\ \gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\ \delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	ε_i^2/N
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	1x10^{-5} day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt\_{}_{phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt\_{}_{prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R[(1)]*, Brigolin D.[(1)], Petrizzo A.[(1)], Zucchetta M.[(2)],

[(1)]Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
[(2)]Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \tag{2}$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\dfrac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \tag{3}$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently "good" model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

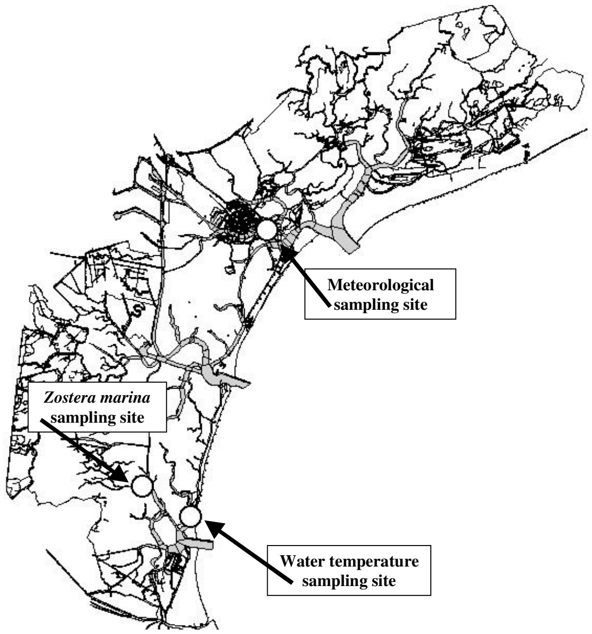

Figure 1. Data sampling sites

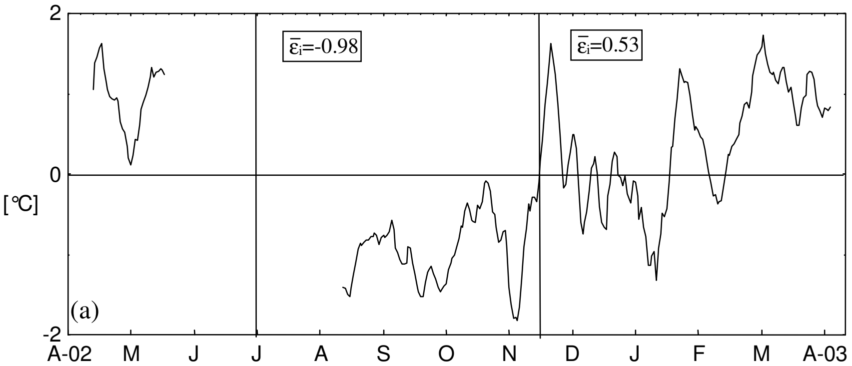

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

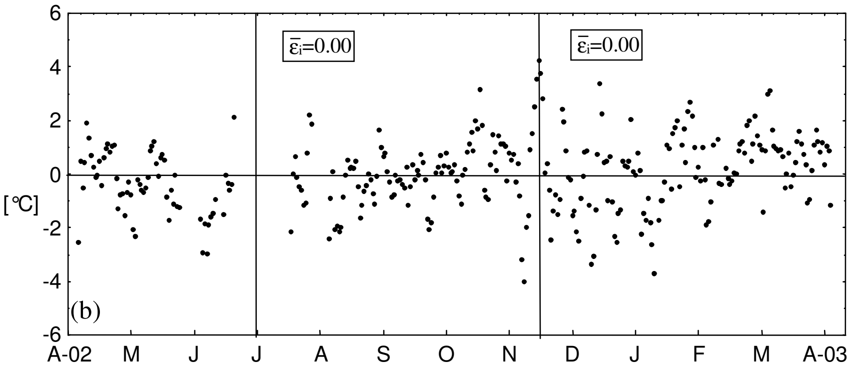

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

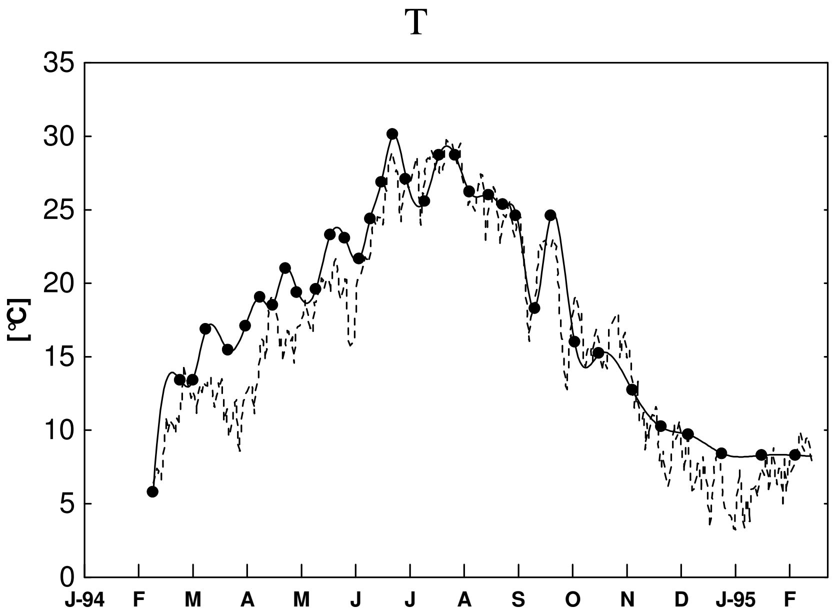

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

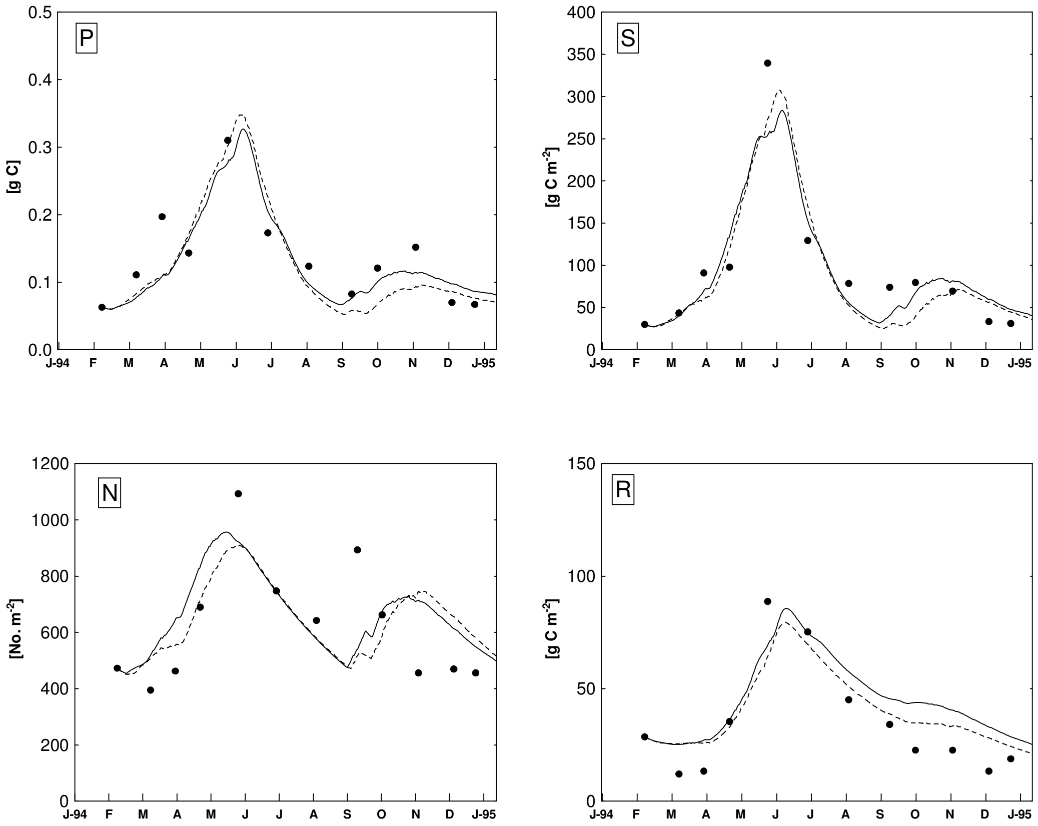

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

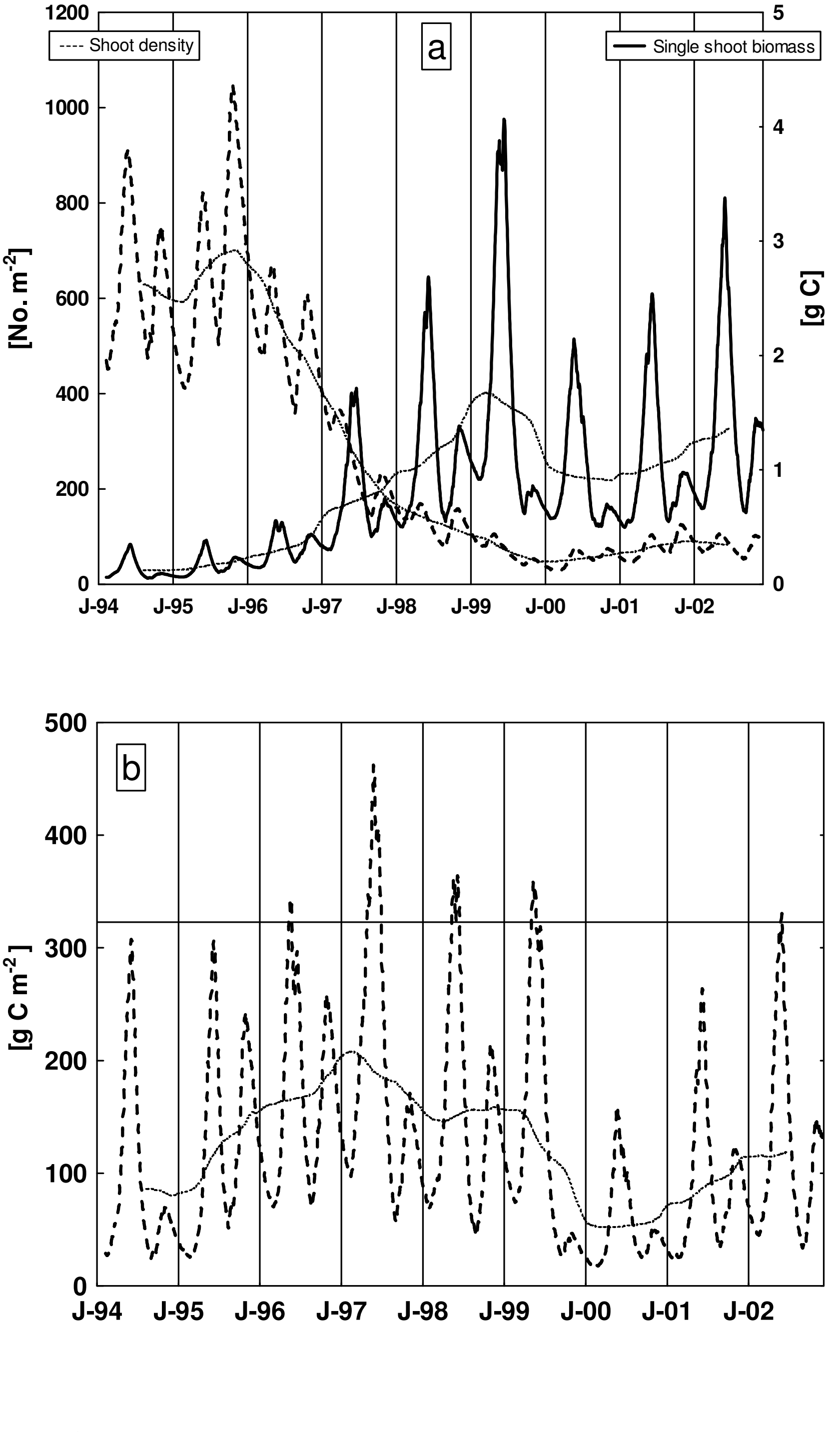

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

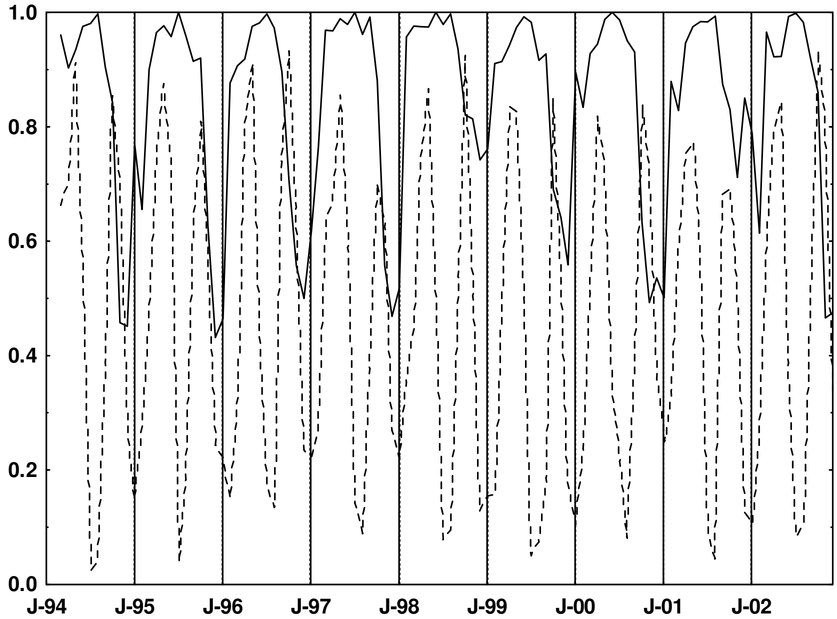

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}^{\ \alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\ \beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}^{\ \gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\ \delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	ε_i^2 / N
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1x10^{-5}$ day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R(1)*, Brigolin D.(1), Petrizzo A.(1), Zucchetta M.(2),

(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a “virtual forecasting” exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently "good" model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat "in the middle" between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

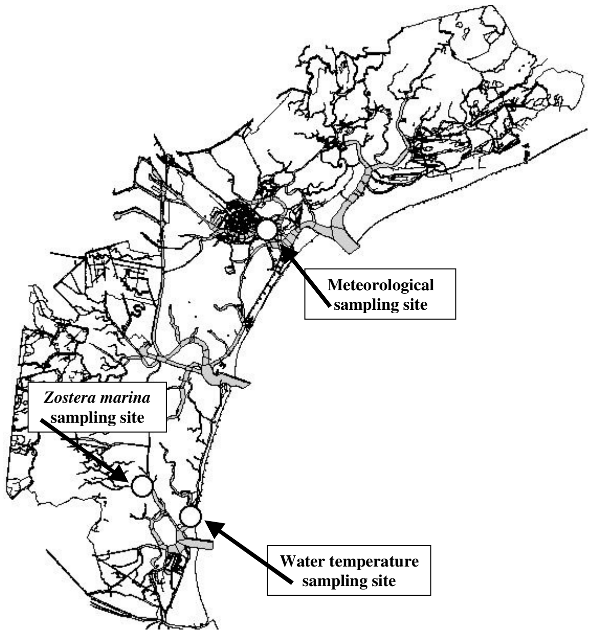

Figure 1. Data sampling sites

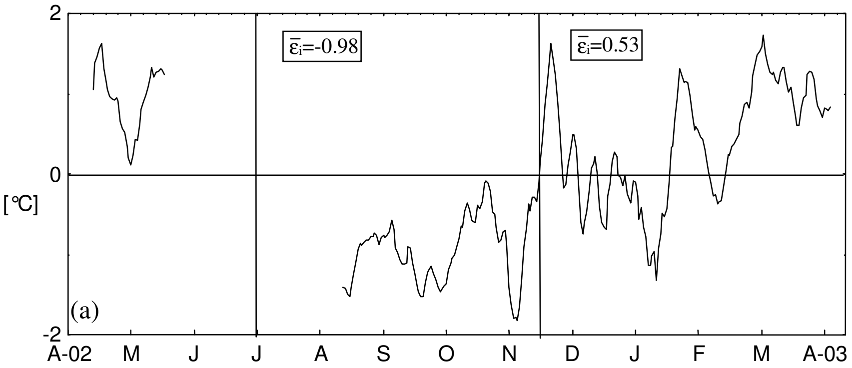

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

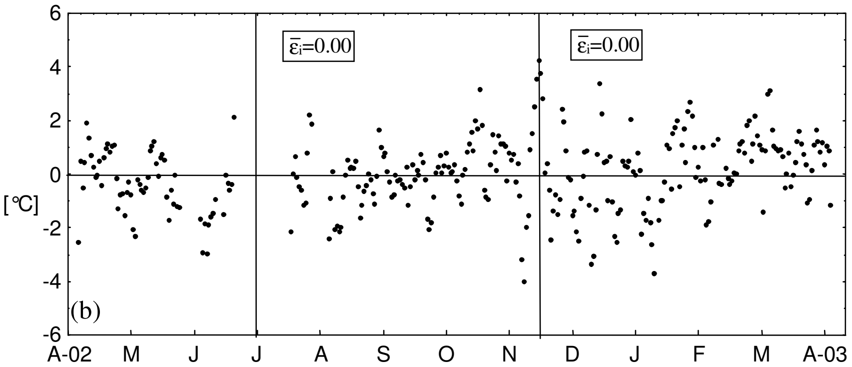

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

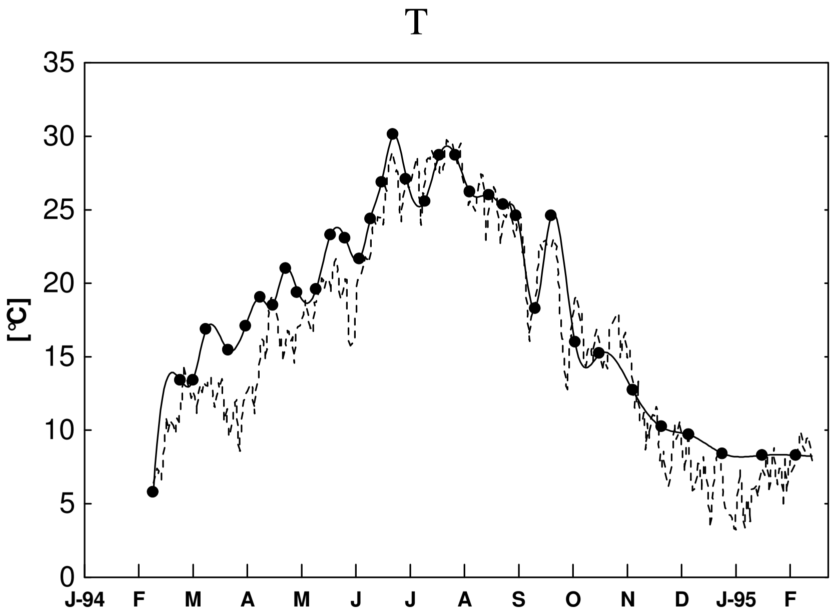

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

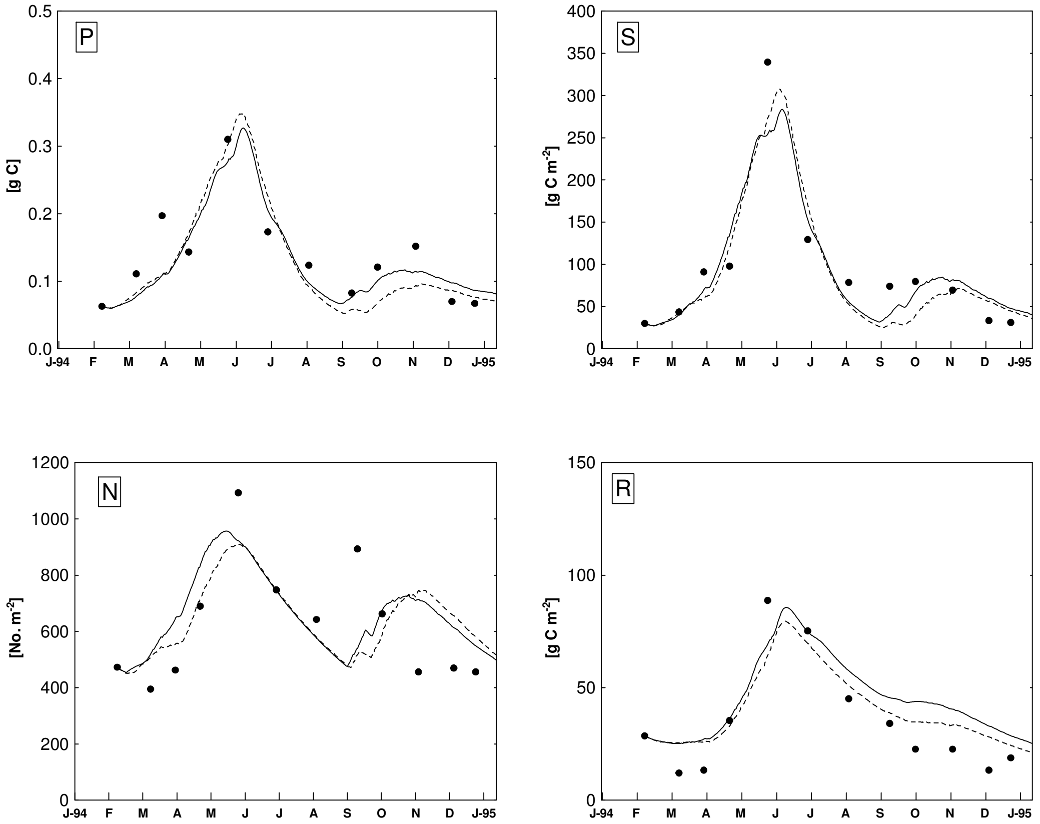

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

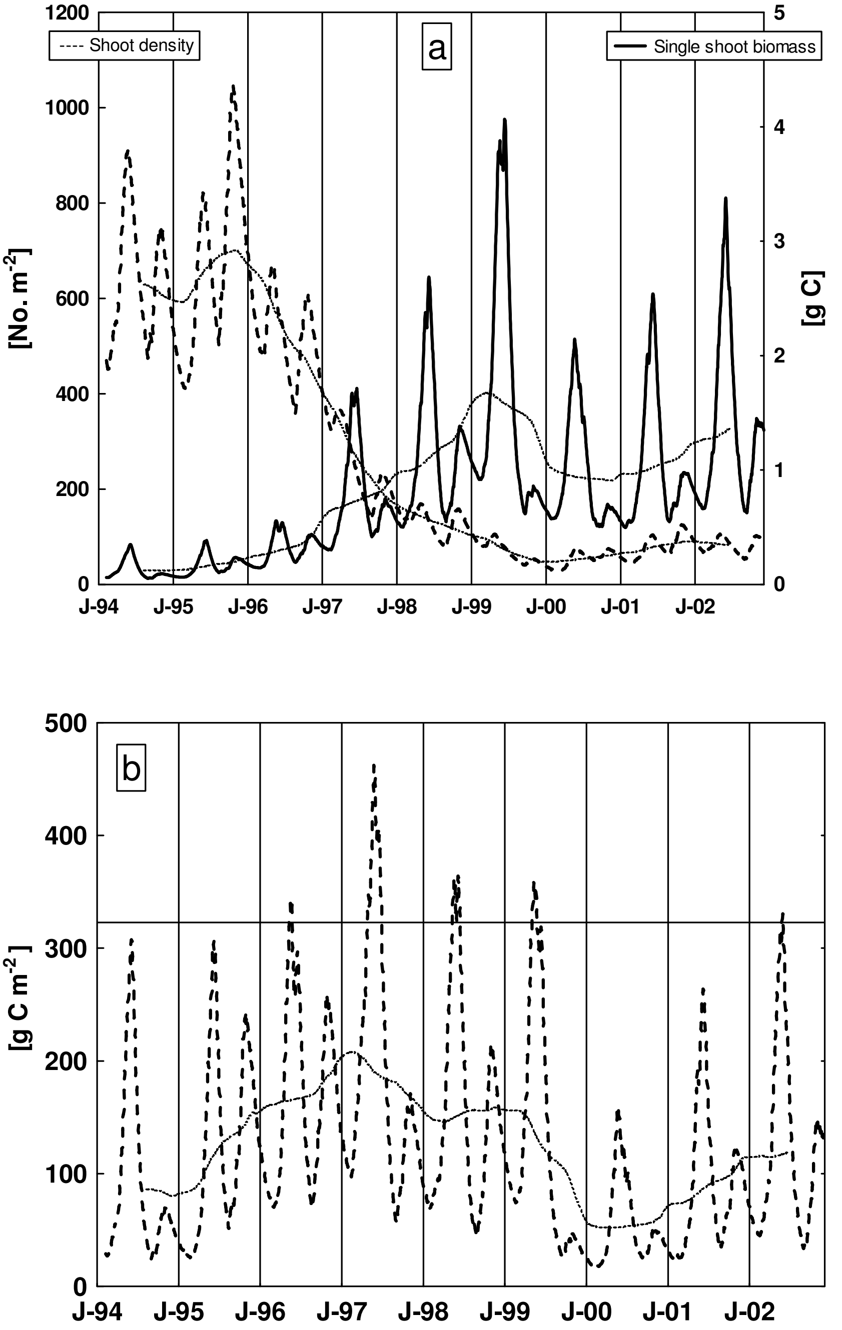

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

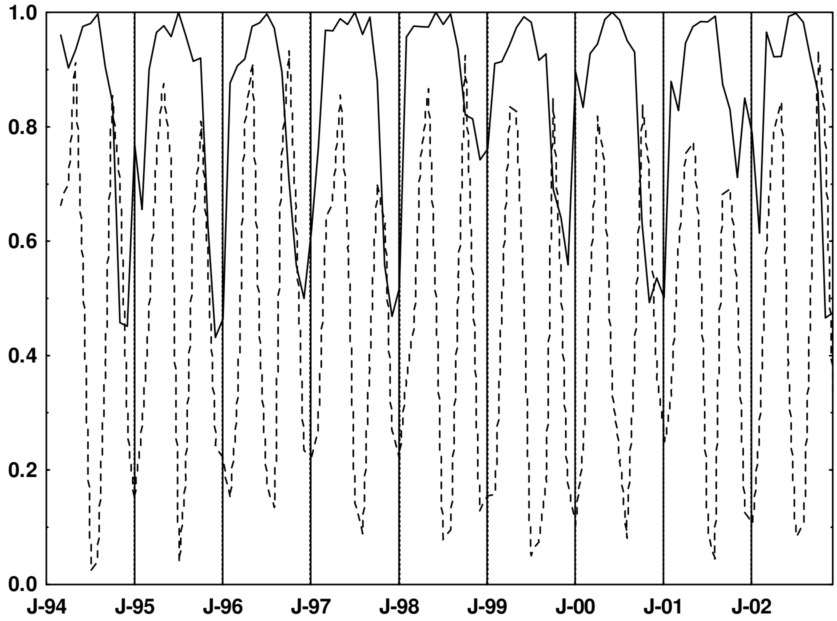

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}{}^{\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}{}^{\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}{}^{\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}{}^{\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	ε_i^2/N
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1x10^{-5}$ day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R(1)*, Brigolin D.(1), Petrizzo A.(1), Zucchetta M.(2),

(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j}(\hat{y}_{i,j} - y_{i,j})^2}{\dfrac{\sum_{i,j}(y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently "good" model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

Acknowledgements

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. ‘Birthday effect’ on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

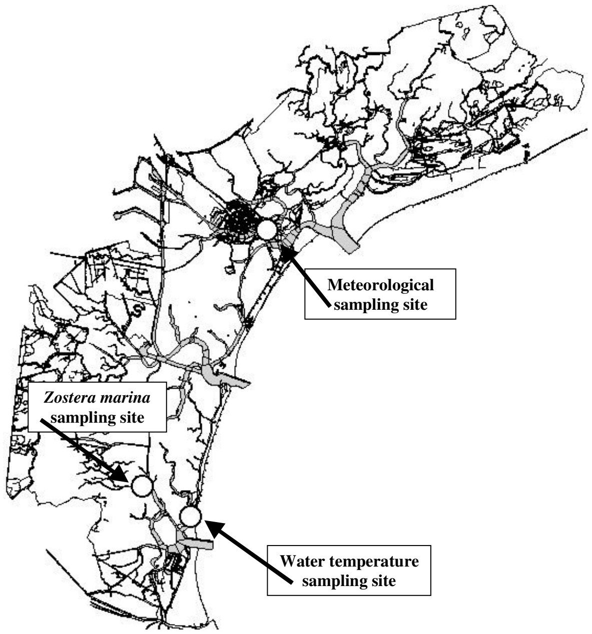

Figure 1. Data sampling sites

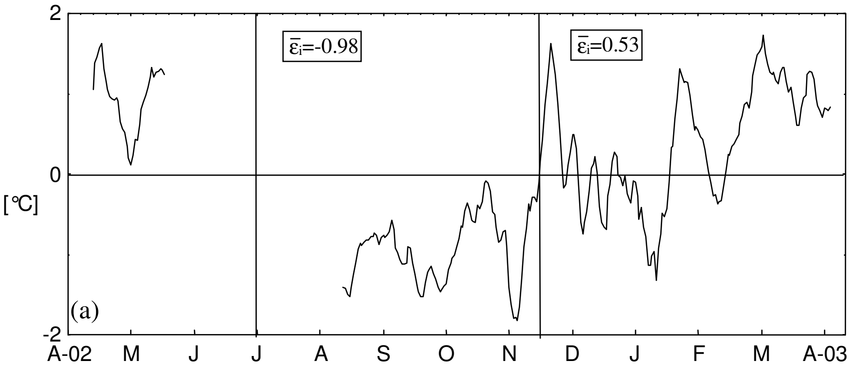

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

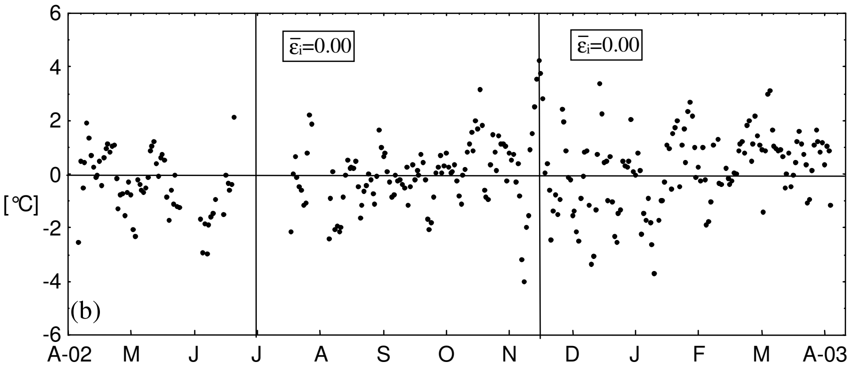

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

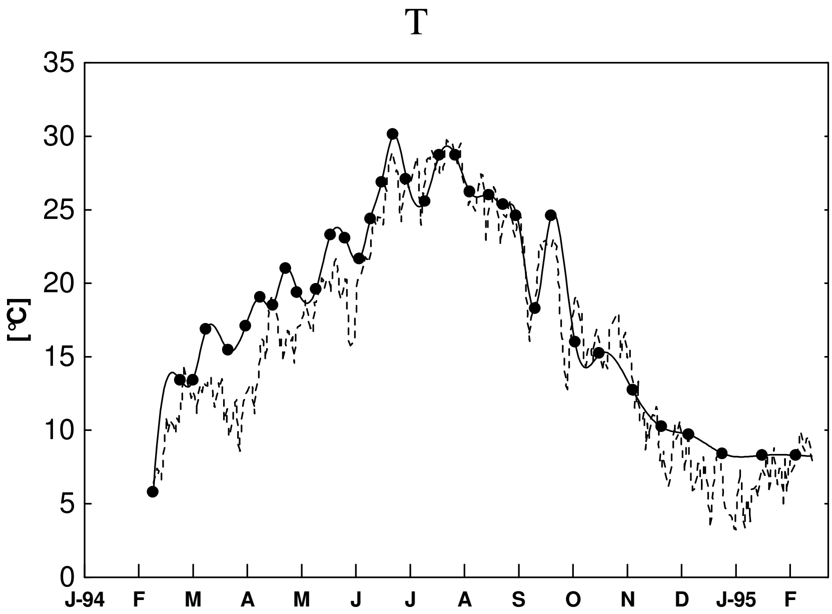

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

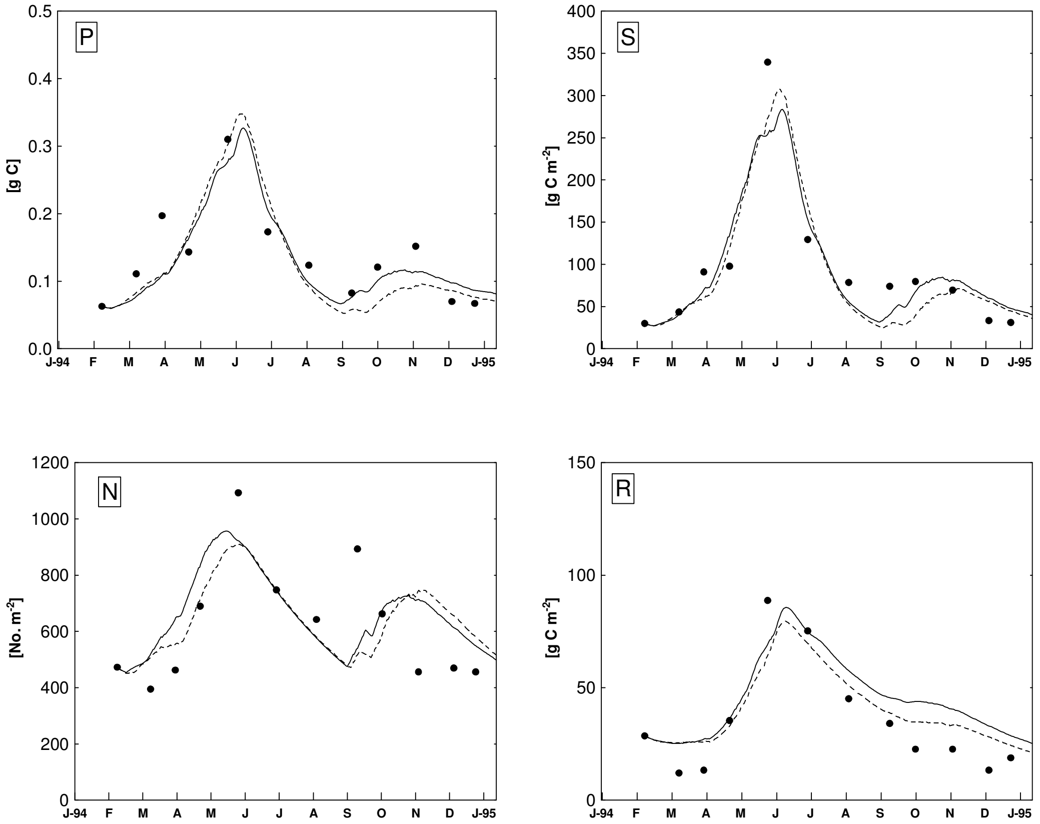

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

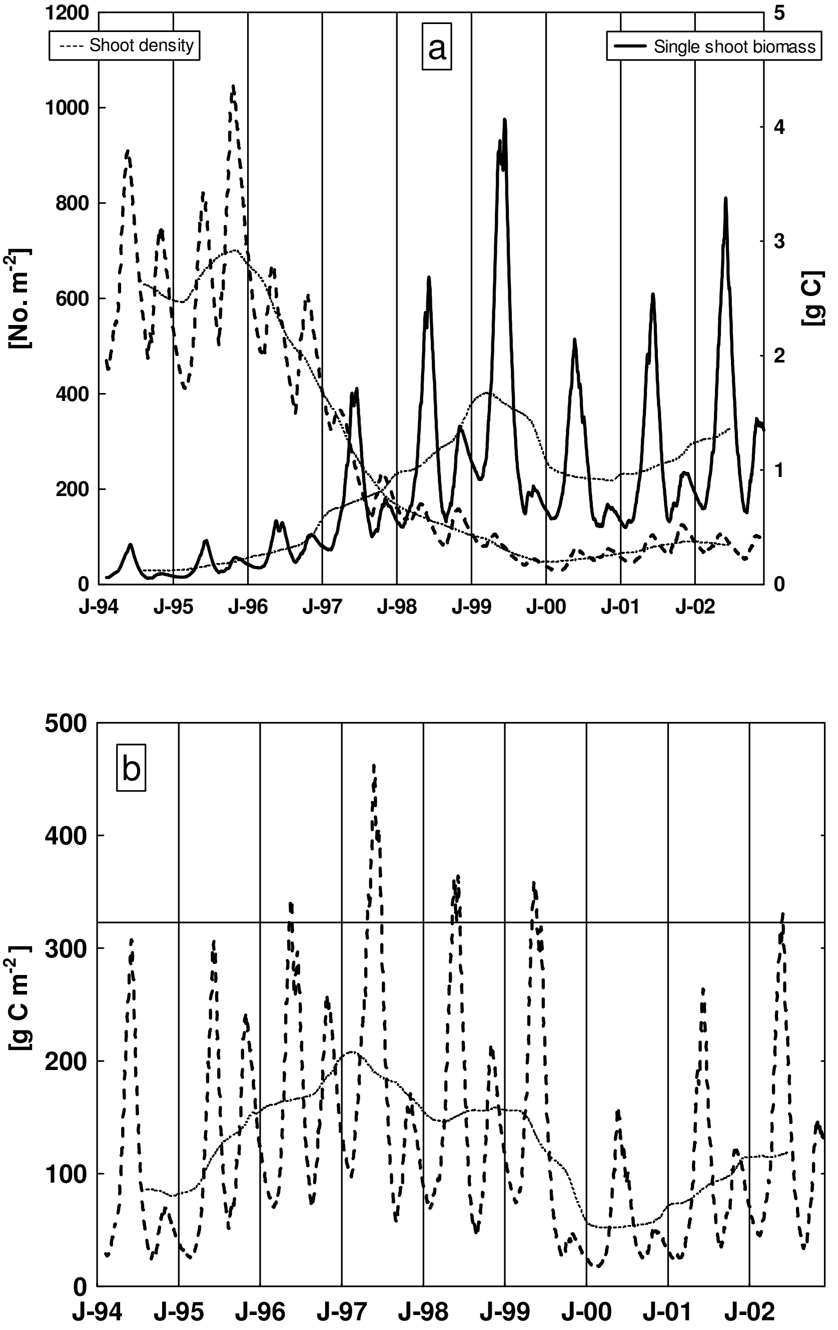

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

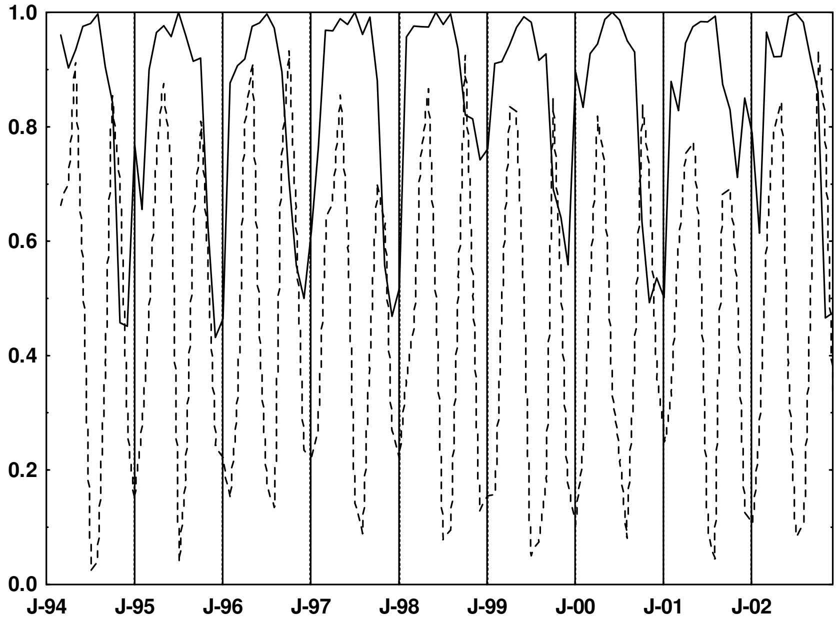

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}{}^{\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}{}^{\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}{}^{\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}{}^{\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	${\varepsilon_i}^2/N$
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	1x10^{-5} day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R[(1)]*, Brigolin D.[(1)], Petrizzo A.[(1)], Zucchetta M.[(2)],

[(1)]Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
[(2)]Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\dfrac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently "good" model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

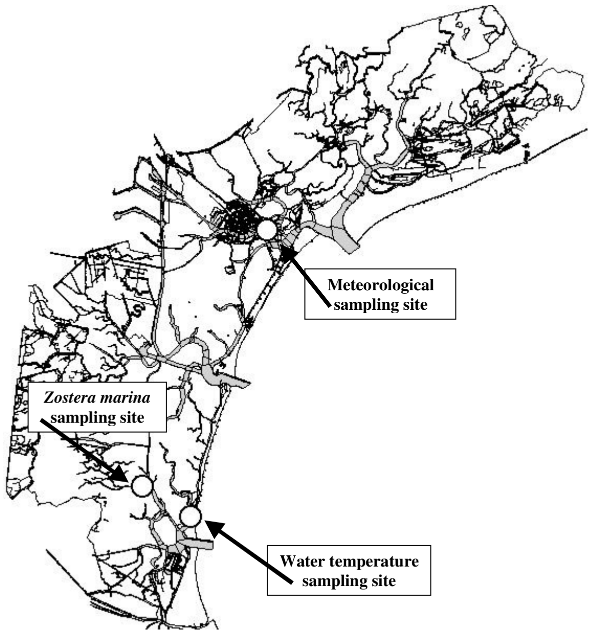

Figure 1. Data sampling sites

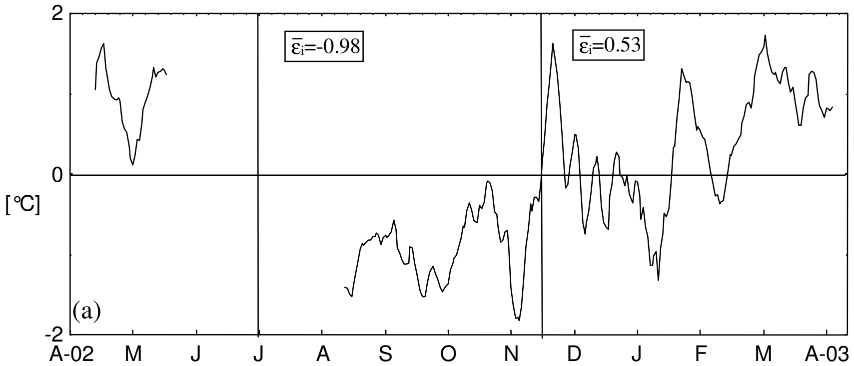

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

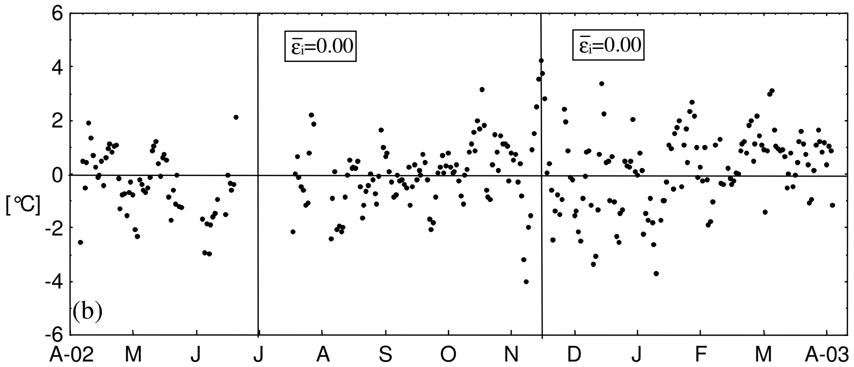

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

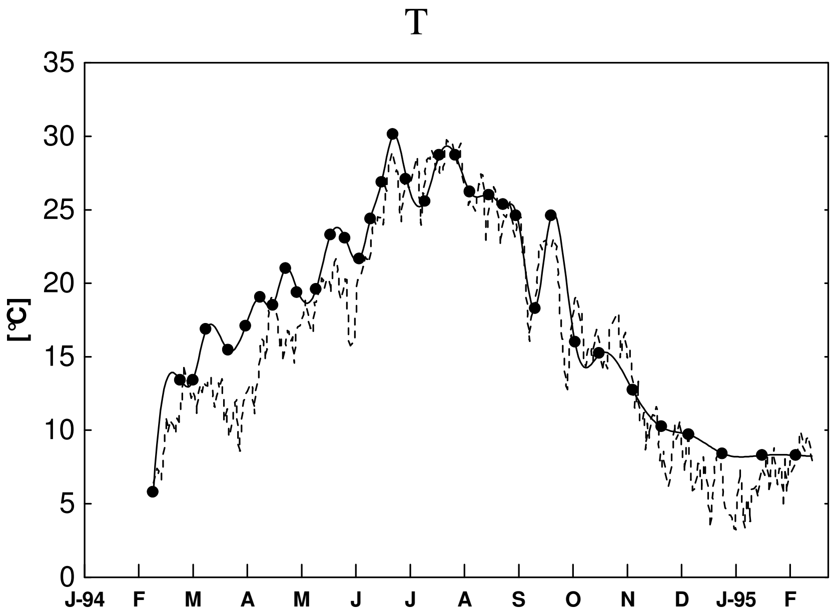

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

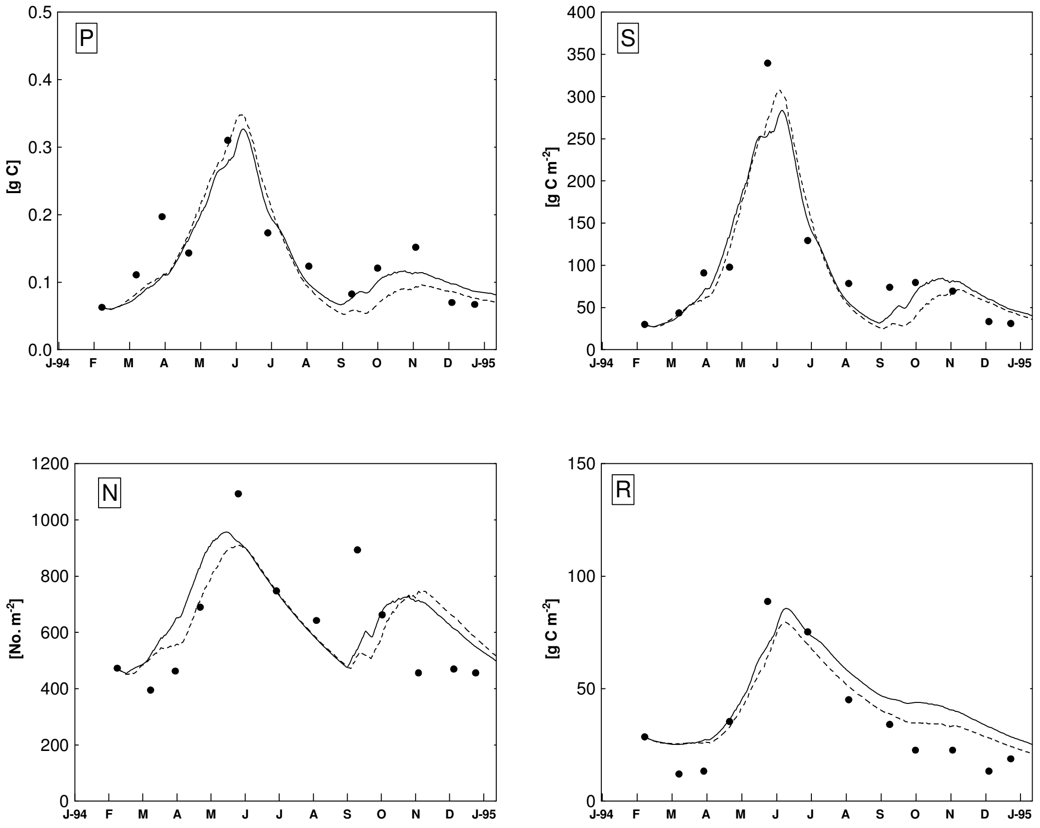

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

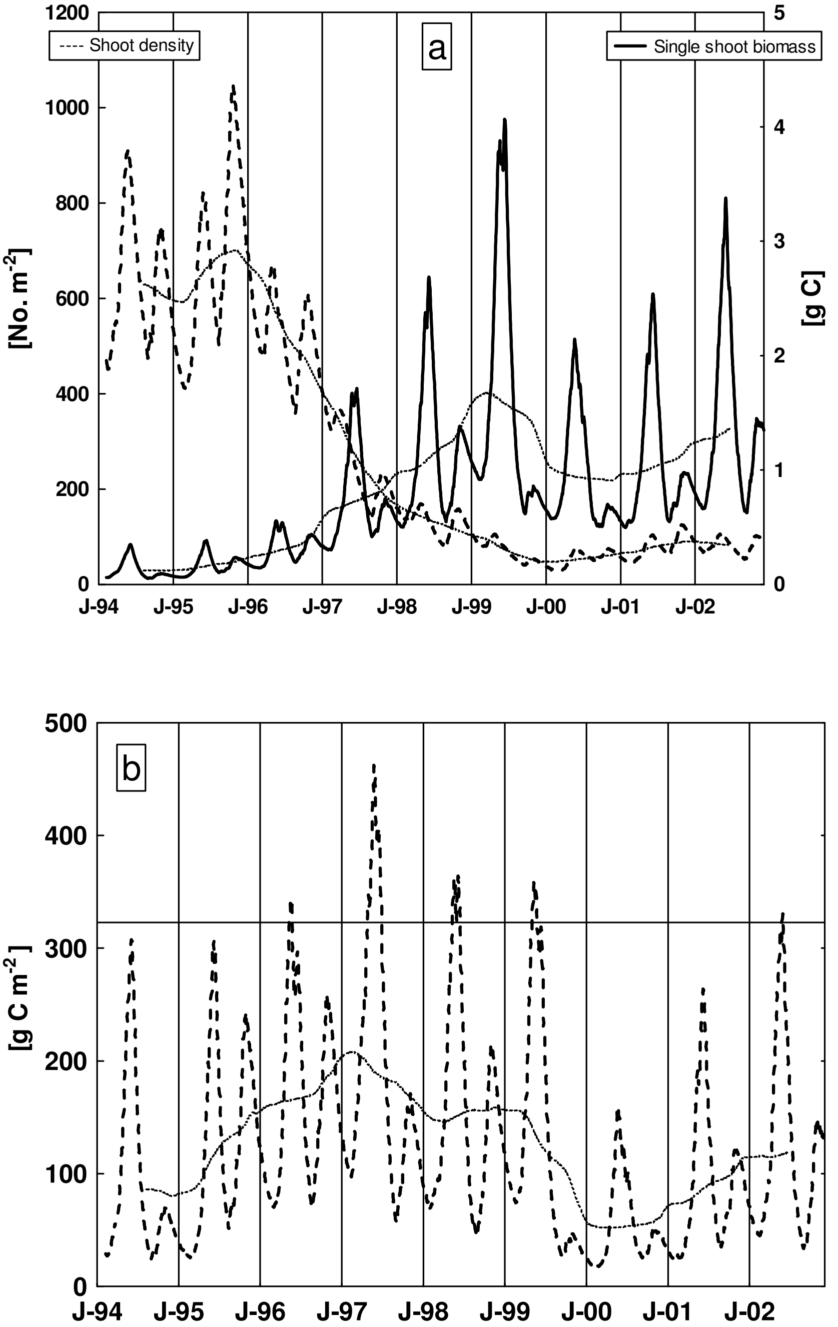

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

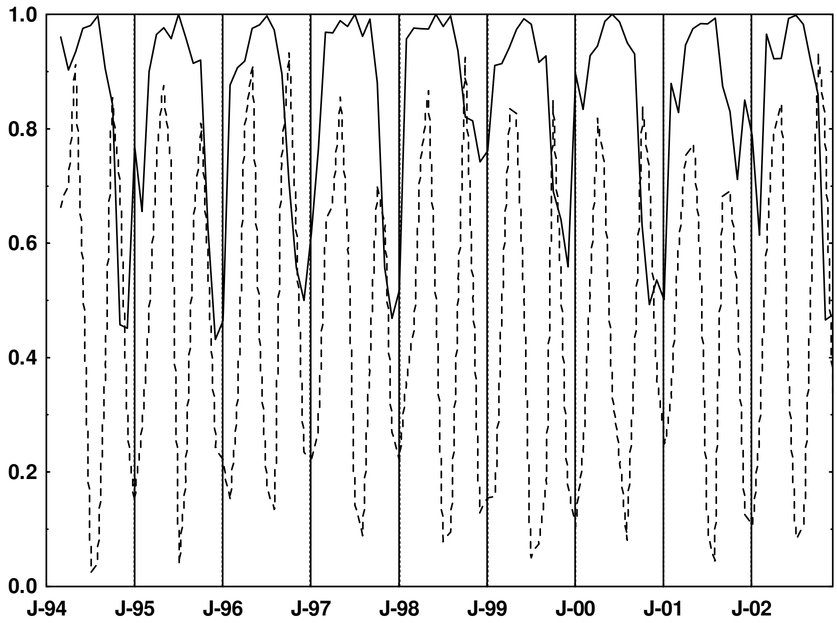

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\;T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\;T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}^{\;\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\;\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}^{\;\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\;\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	$\varepsilon_i^{\ 2}/N$
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	1x10^{-5} day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R(1)*, Brigolin D.(1), Petrizzo A.(1), Zucchetta M.(2),

(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \tag{3}$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently "good" model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

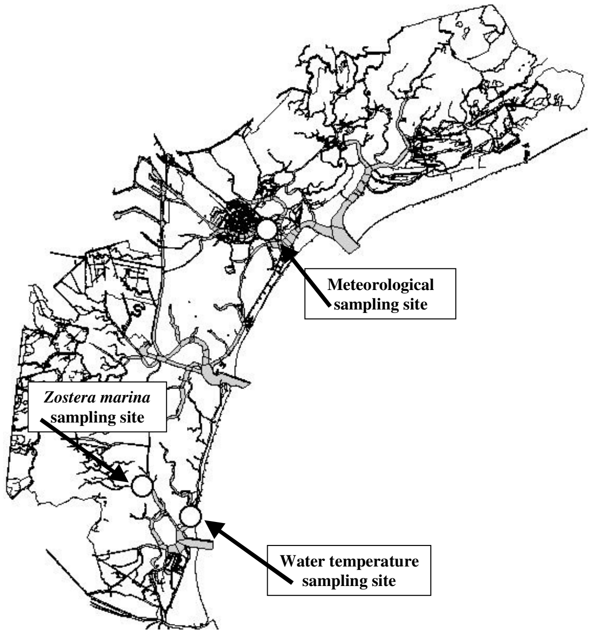

Figure 1. Data sampling sites

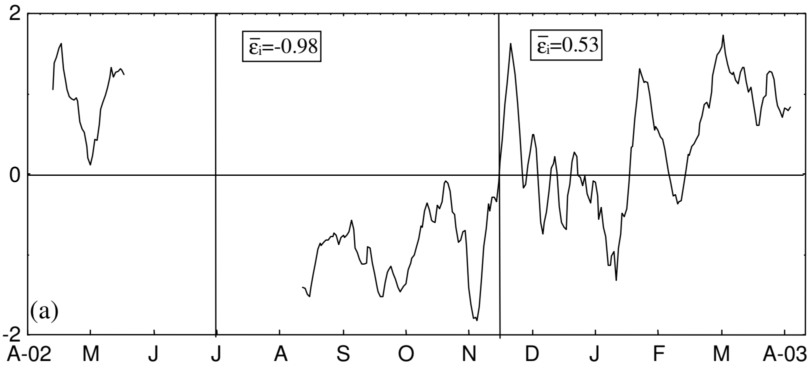

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

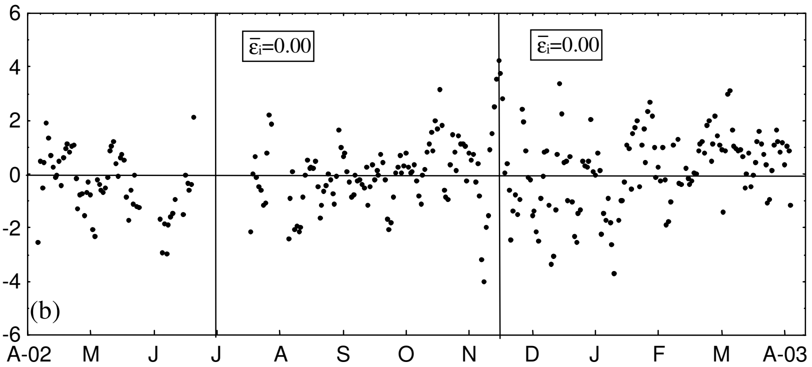

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

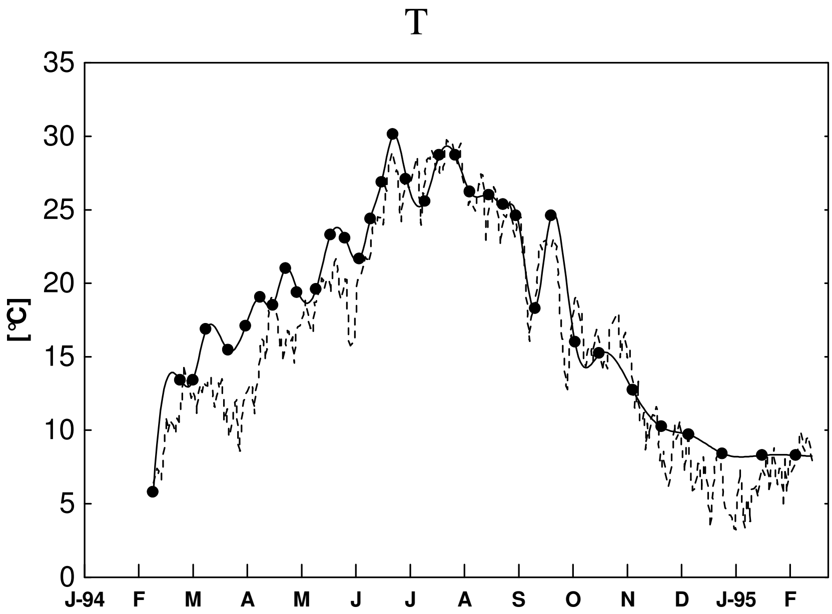

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

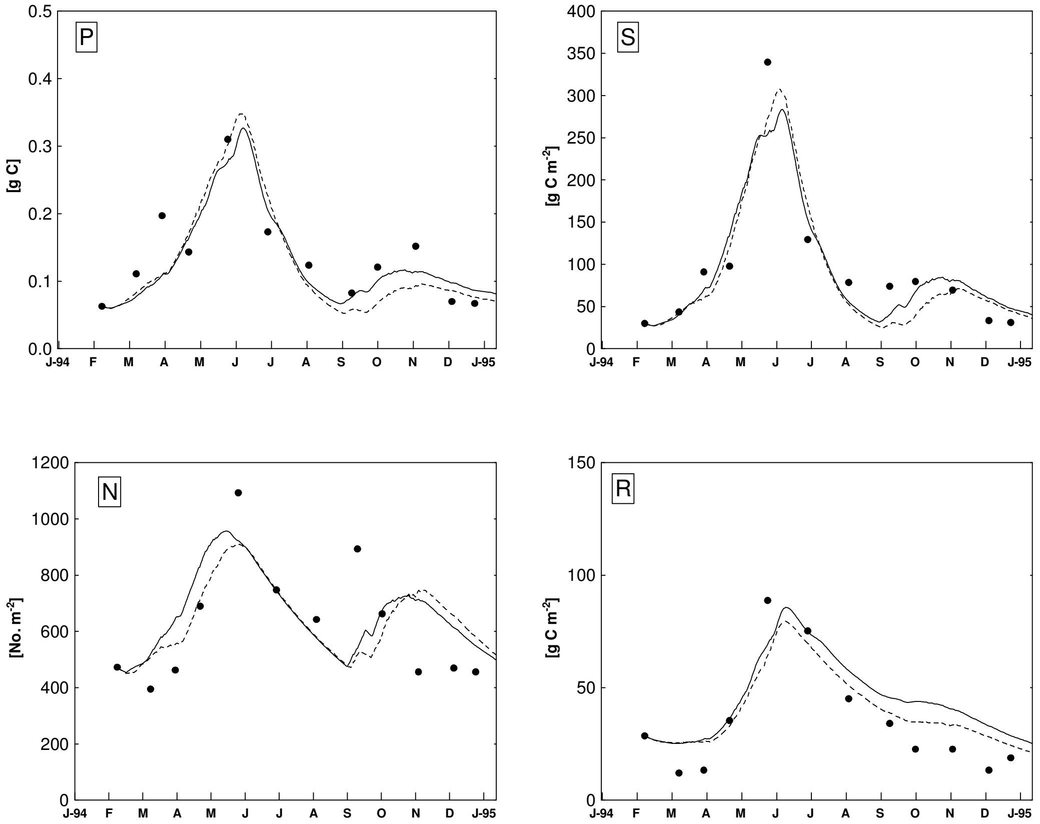

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

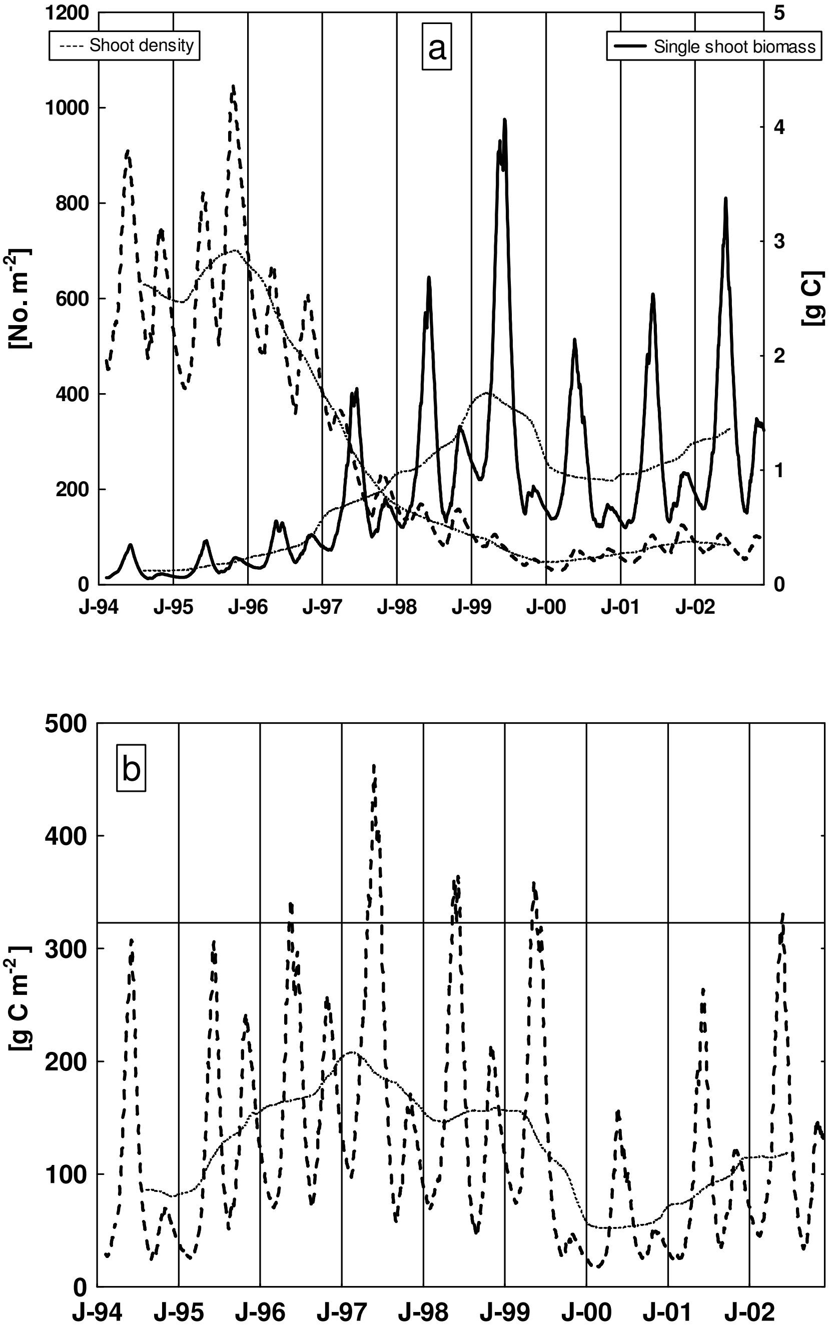

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

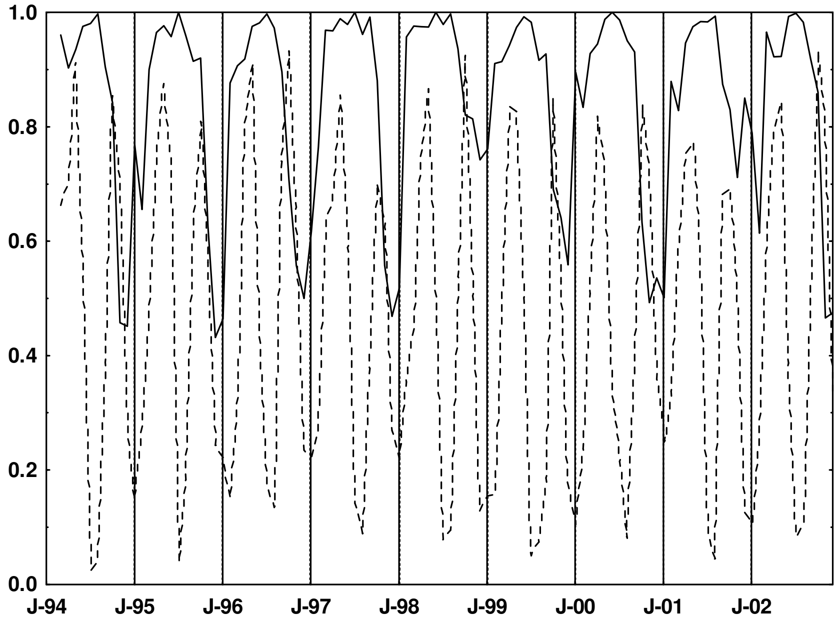

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}^{\;\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\;\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}^{\;\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\;\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec\,(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	$\varepsilon_i^{\,2}/N$
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1x10^{-5}$ day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt\_{}_{phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt\_{}_{prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R^(1)*, Brigolin D.^(1), Petrizzo A.^(1), Zucchetta M.^(2),

^(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
^(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as "archives of hypothesis", since the model structure and our "a priori" estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The "calibration" procedure establishes a relationship between the "theory" and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the "unobserved components" (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \tag{2}$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The *I* and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\frac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where *i* is the number of observations and *j* the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently “good” model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

Acknowledgements

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

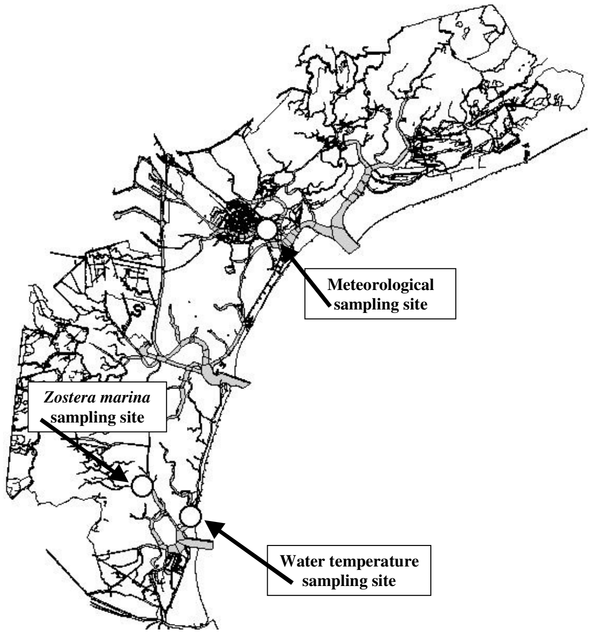


Figure 1. Data sampling sites

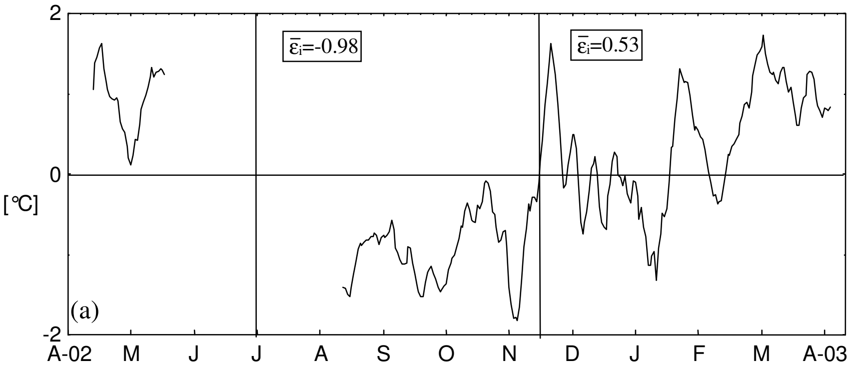


Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

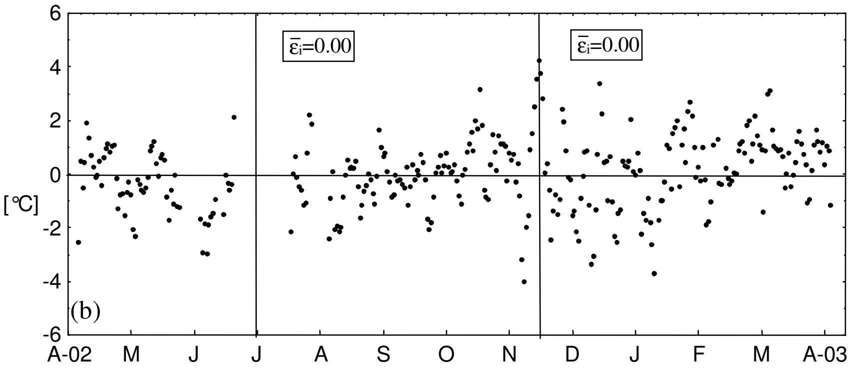


Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

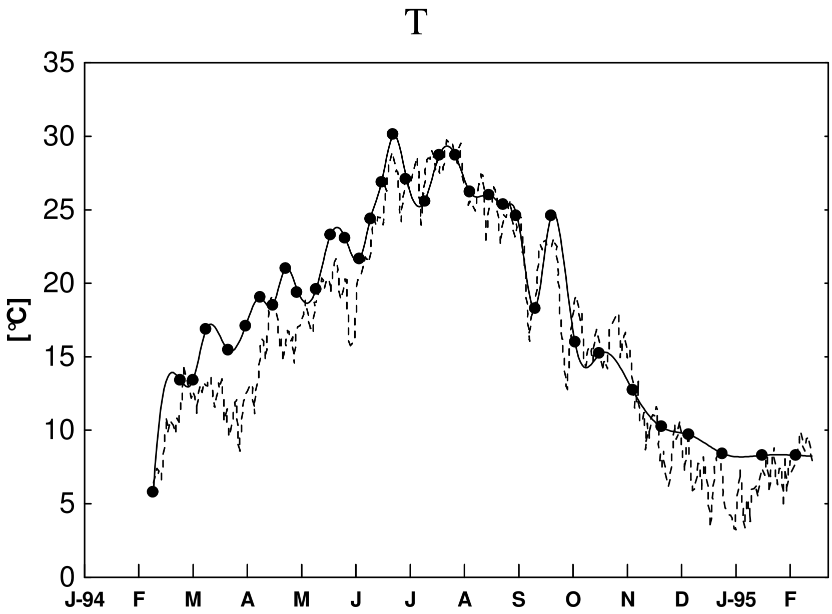


Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

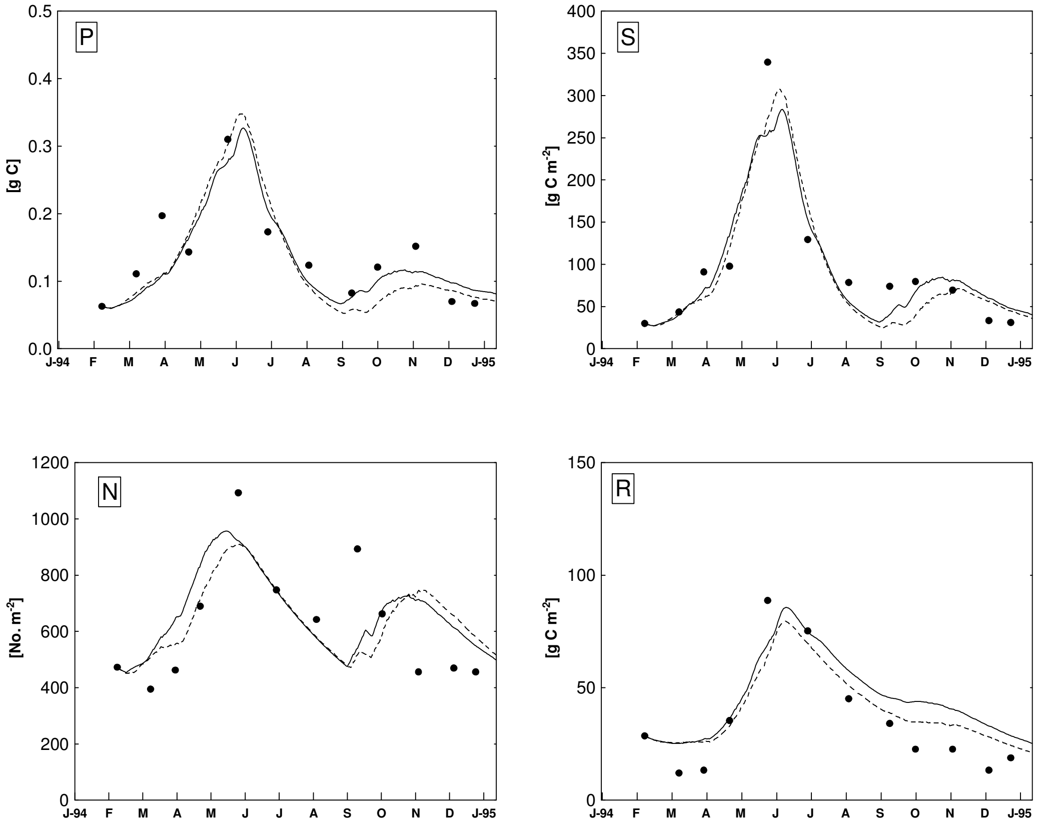
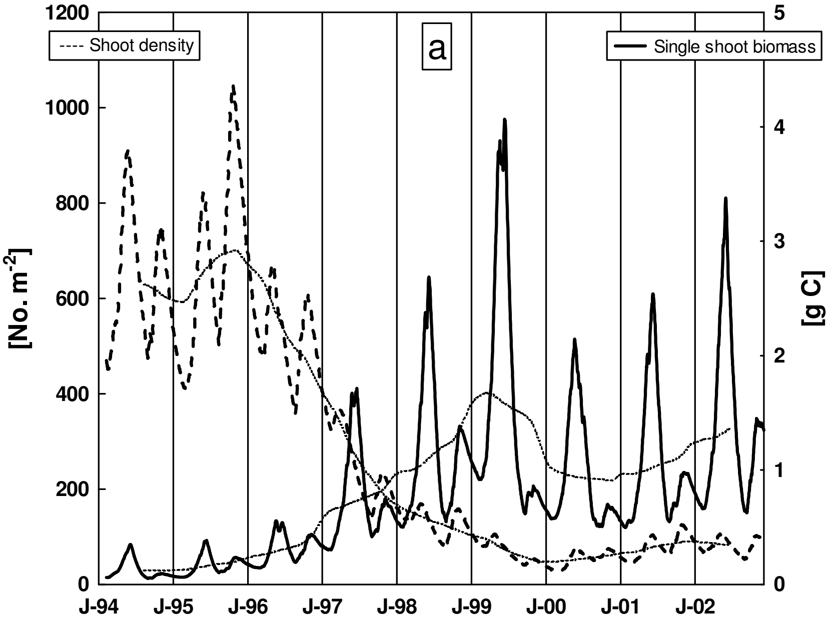


Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.



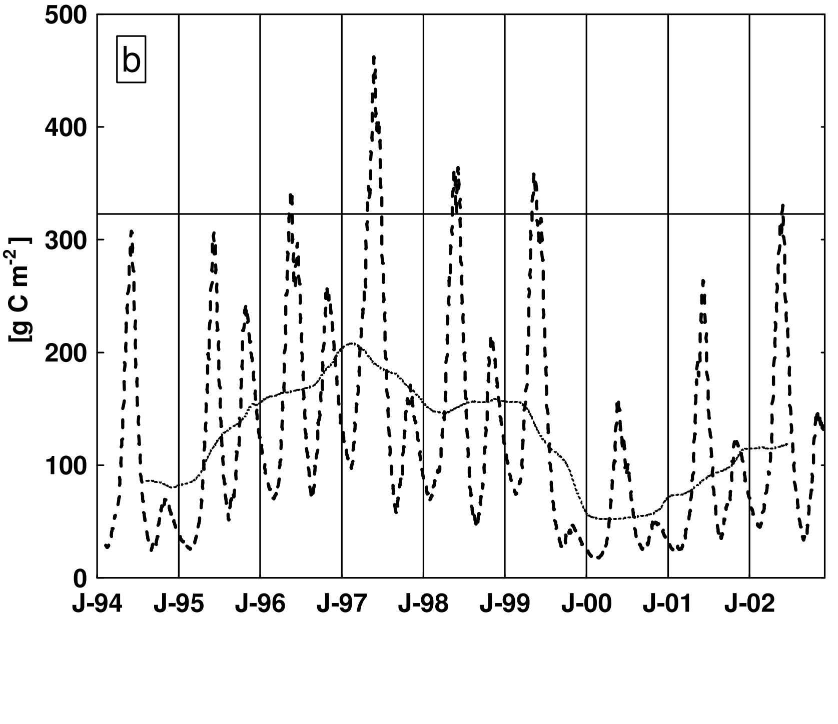


Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

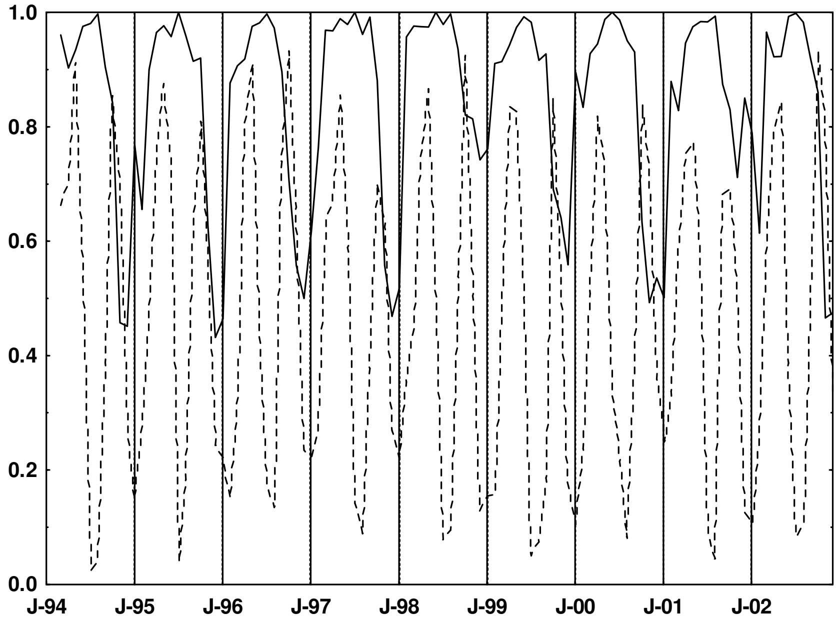


Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}^{\ \alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\ \beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}^{\ \gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\ \delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	$\varepsilon_i^{\,2}/N$
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	1x10^{-5} day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R[(1)]*, Brigolin D.[(1)], Petrizzo A.[(1)], Zucchetta M.[(2)],

[(1)]Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
[(2)]Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as “archives of hypothesis”, since the model structure and our “a priori” estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The “calibration” procedure establishes a relationship between the “theory” and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the “unobserved components” (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a "virtual forecasting" exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The I and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j} (\hat{y}_{i,j} - y_{i,j})^2}{\dfrac{\sum_{i,j} (y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where i is the number of observations and j the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently "good" model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

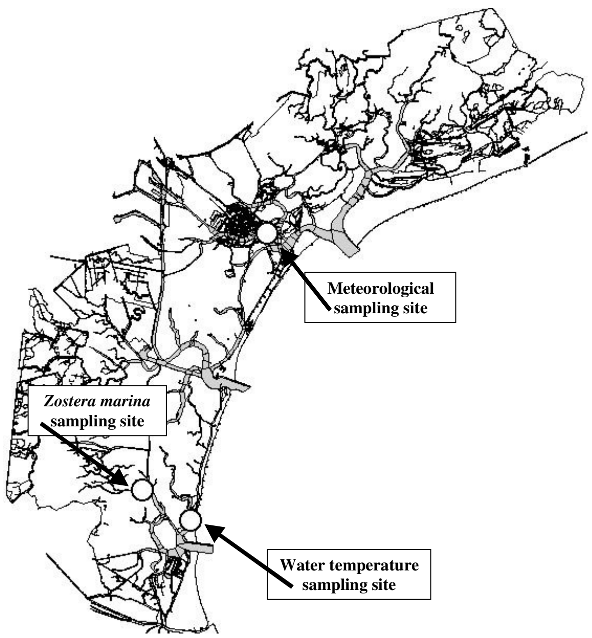

Figure 1. Data sampling sites

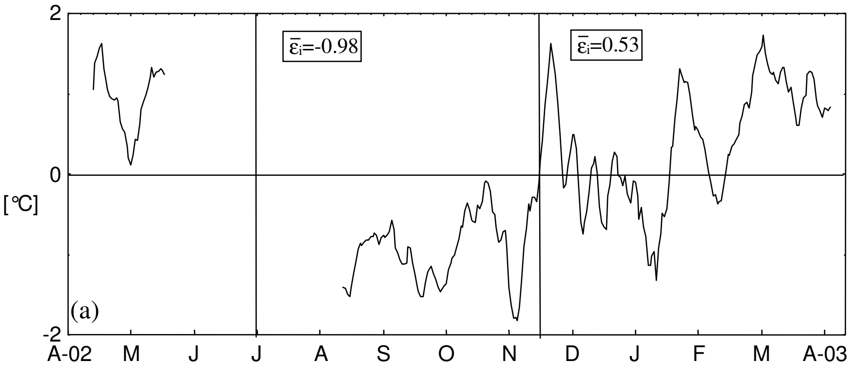

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

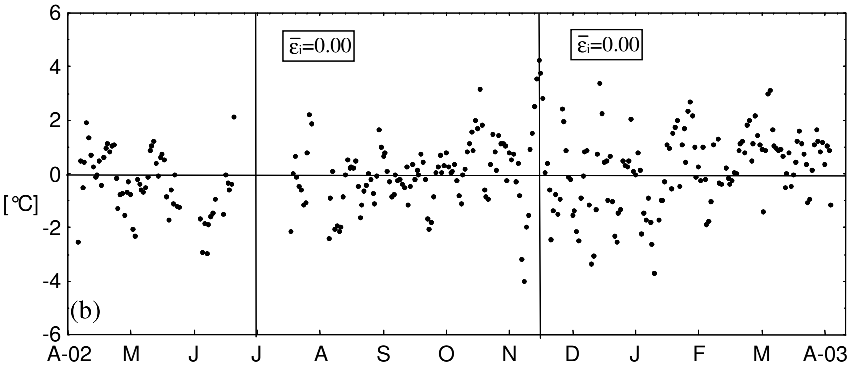

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

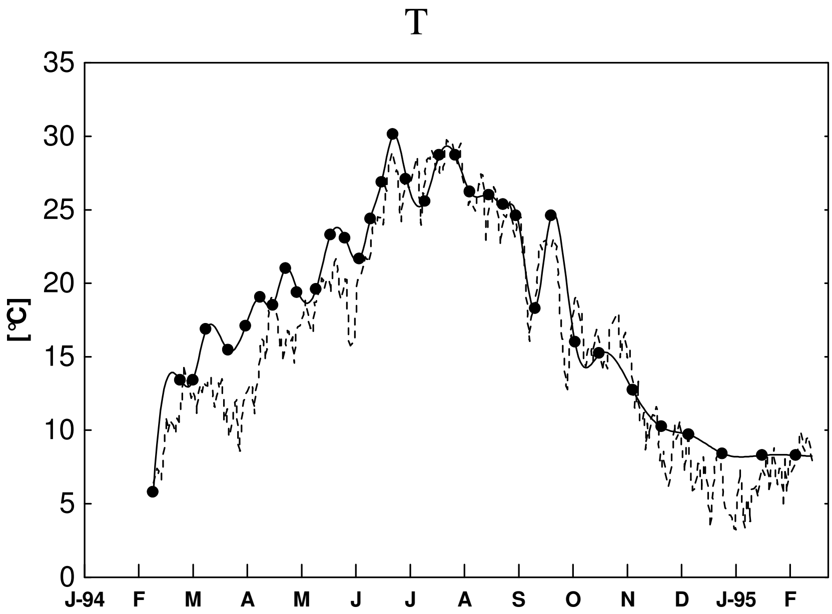

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

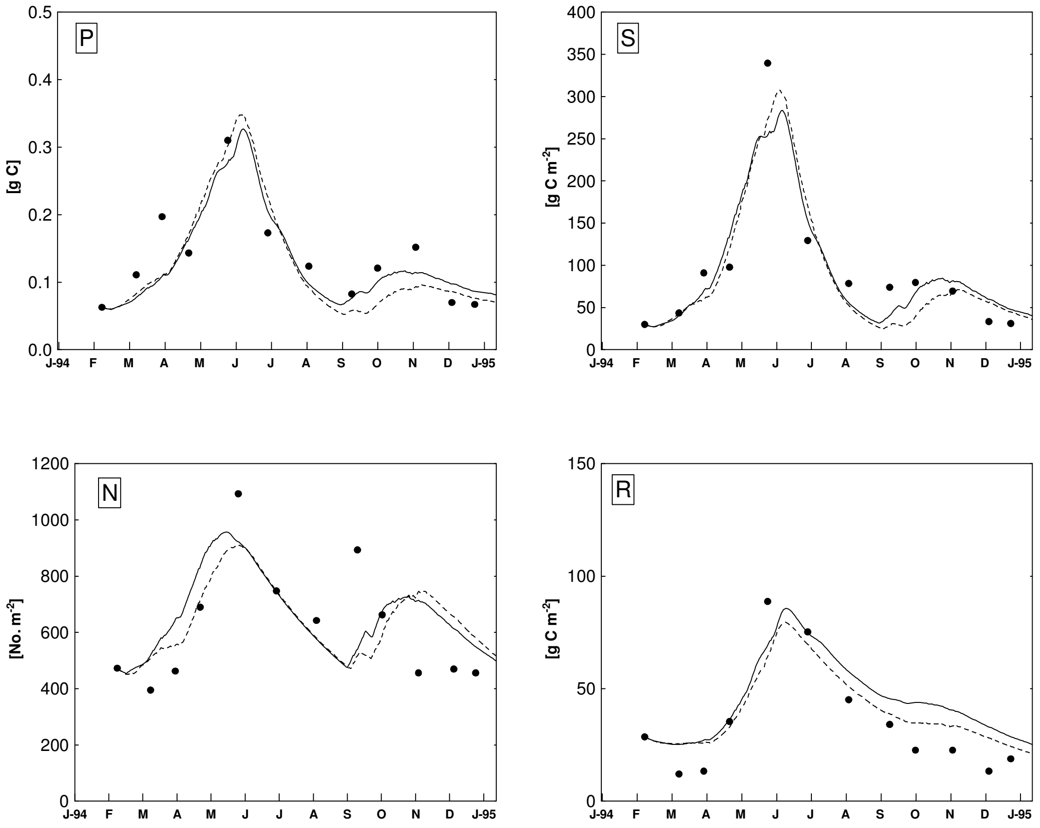

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

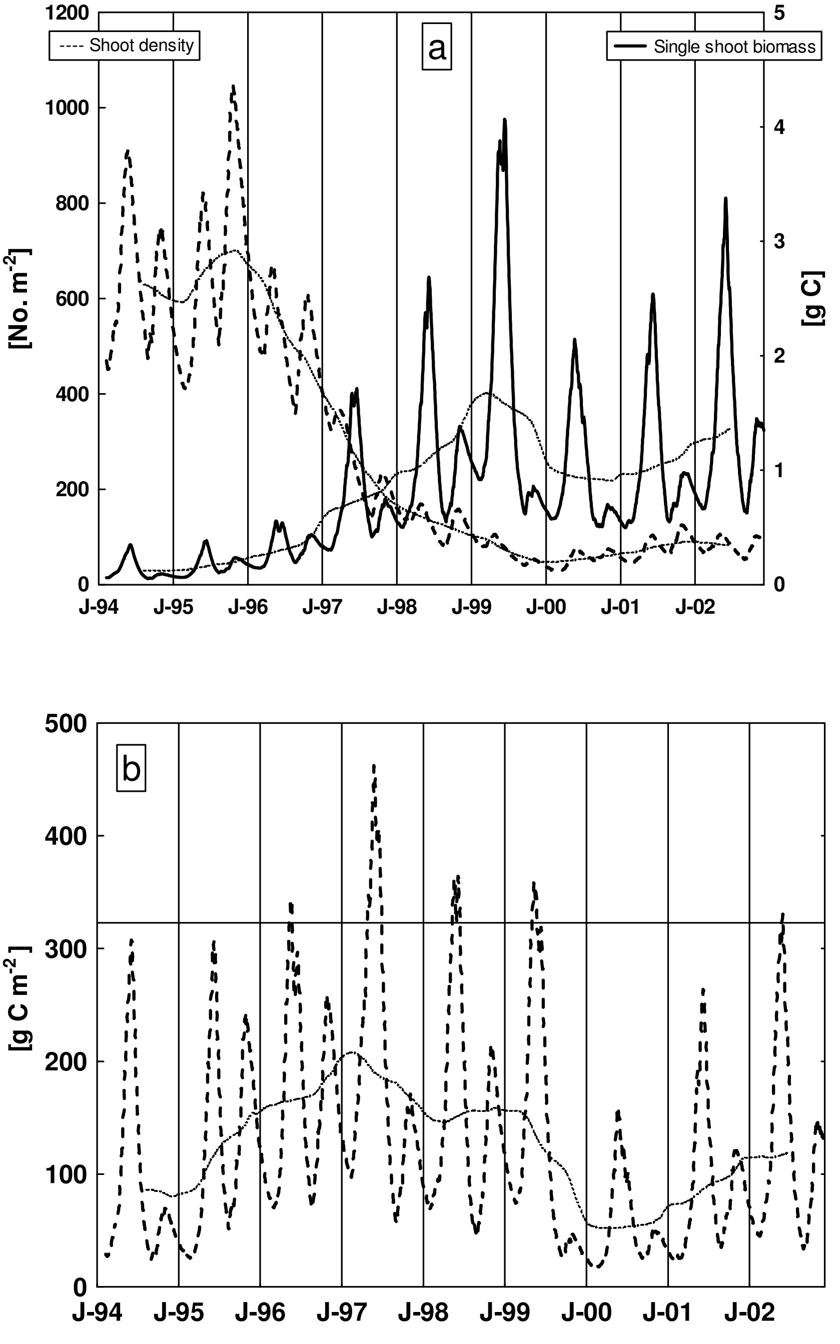

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

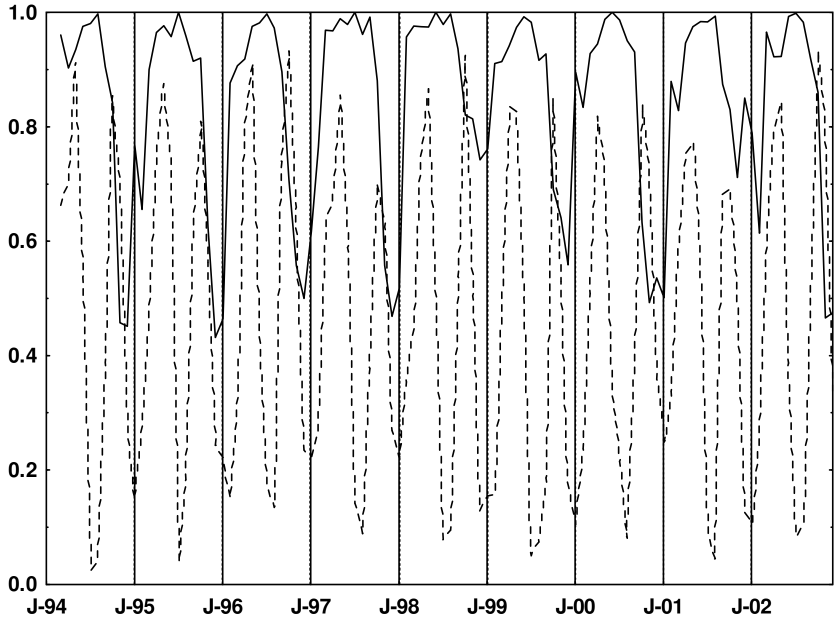

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}(T_w) = \begin{cases} k_{0\_phot}^{\;\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}^{\;\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}} \right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}} \right)^{stt\_phot}$$

$$f_{\_prod}(T_w) = \begin{cases} k_{0\_prod}^{\;\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}^{\;\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}} \right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}} \right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma} \right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{\,T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	${\varepsilon_i}^2/N$
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter	Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph} °C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod} °C	20.0	23.0				
	σ gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	7.2 10^{-3} day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1x10^{-5}$ day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.

Testing the robustness of primary production models in shallow coastal areas: a case study

Pastres, R(1)*, Brigolin D.(1), Petrizzo A.(1), Zucchetta M.(2),

(1)Dipartimento di Chimica Fisica, Università Ca' Foscari, Venezia, Italy
(2)Dipartimento di Scienze Ambientali, Università Ca' Foscari, Venezia, Italy
*Corresponding author: Dipartimento di Chimica Fisica, Dorsoduro 2137, 30123 Venezia, Italy. e-mail:pastres@unive.it

Abstract

In this paper we investigate the robustness of a dynamic model, which describes the dynamic of the seagrass *Zostera marina,* with respect to the inter-annual variability of the two main forcing functions of primary production models in eutrophicated environments. The model was previously applied to simulate the seasonal evolution of this species in the Lagoon of Venice during a specific year and calibrated against time series of field data. In the this paper, we present and discuss the results which were obtained by forcing the model using time series of site-specific daily values concerning the solar radiation intensity and water temperature. The latter was estimated by means of a regression model, whose input variable was a site-specific time series of the air temperature. The regression model was calibrated using a year-long time series of hourly observations. The *Zostera marina* model was first partially recalibrated against the same data set that was used in the original paper. Subsequently, the model was forced using a seven-year long time series of the driving functions, in order to check the reliability of its long-term predictions. Even though the calibration gave satisfactory results, the multi-annual trends of the output variables were found to be in contrast with the observed evolution of the seagrass biomasses. Since detailed information about the air temperature and solar radiation are often available, these findings suggest that the testing of the ecological consistency of the evolution of primary production models in the long term would provide additional confidence in their results, particularly in those cases in which the scarcity of field data does not allow one to perform a formal corroboration/validation of these models.

Keywords: model robustness, *Zostera marina*, Lagoon of Venice

1. Introduction

According to (Beck, 1987) dynamic models can be thought of as "archives of hypothesis", since the model structure and our "a priori" estimates of the parameters, forcing functions, and initial and boundary conditions summarize our theoretical knowledge and hypotheses about the dynamic of a given system and its interactions with the surroundings. The "calibration" procedure establishes a relationship between the "theory" and a given set of observations, since it leads to the estimation of a subset of parameters, which can be thought of as the "unobserved components" (Young, 1998) of the dynamic system, by fitting the model output to a specific set of output data. From this point of view, the trajectory of a calibrated dynamic model can be considered as the result of the integration of general principles with specific empirical information concerning the sampling site where the model was applied. In order to increase the confidence in the model output, the modelling practice suggests that the model should be corroborated/validated by comparing its output with sets of data other then those used for calibrating it. However, in many instances, particularly in the field of ecological and environmental modelling, the lack of data does not allow for the execution of a formal corroboration/validation of the model. Nonetheless, the literature offers several examples (Wortmann et. al., 1998, Bearlin et. al., 1999) in which calibrated models are proposed for further applications, based on the implicit assumption that their results would be, at least, qualitatively sound, if they were forced with time series of input functions which were not too different from those used in the calibration.

The concept of robustness can be defined in several ways (see for example, www.discuss.santafe.edu/robustness): according to Gribble (2001), it is the ability of a system to continue to operate correctly across a wide range of operation conditions. As far as primary production models in coastal areas are concerned, the water temperature and solar radiation intensity can certainly be considered the two fundamental forcing functions affecting photosynthetic rates. These factors become even more important as regards eutrophic basins, where the photosynthetic rates are seldom reduced by a lack of the dissolved inorganic forms of N and P. Since these driving functions are explicitly taken into account by the large majority of primary production models, one can expect that the results of these models, once they had been calibrated against time series of field data, should be robust, at least, with respect to the inter-annual variability of the water temperature and the intensity of the solar radiation which characterize the calibration site. In this paper, we suggest that further support

should be given to the results obtained by means of model calibration/validation, by investigating the long-term behaviour of the model trajectory. The multi-annual evolutions of the state variables were computed by forcing the model using multi-annual time series of the daily or hourly values of the solar radiation intensity and the water temperature. It should be stressed here that such an analysis does not require additional field data, but can be performed using time series of the solar radiation and air temperature which are often available because these parameters are collected routinely by the local automatic weather stations. In fact, these data can be used for predicting the water temperature in shallow lakes and coastal lagoons with sufficient accuracy since, in these basins, the evolution of this variable is largely conditioned by the heat exchanges with the atmosphere (Dejak et al., 1992).

In this paper, we provide evidence that this simple analysis may give interesting results by investigating the long-term behaviour of the trajectories of an ODE model, which simulates the dynamic of the seagrass *Zostera marina*. The model has already been proposed (Zharova et al., 2001), and was applied to the simulation of the evolution of the *Zostera marina* shoot and root/rhizome biomass densities in the Lagoon of Venice. The paper presented the results of the calibration of some of the key parameters based on time series of biomasses that were collected in 1994-95, while the role of the forcing functions was also discussed to a certain extent. However, the issues of model validation/corroboration and model robustness were not addressed. Therefore, we had to think about other ways of testing this model, with a view to include the seagrass dynamics in a 3D transport-reaction model (Pastres et al., 2001). In order to accomplish this task, we performed a “virtual forecasting” exercise to check the consistency of the biomasses trajectories during the period 1996-2002. The execution of this test required the estimation of the forcing functions during the period 1994-2002. The time series of the solar radiation intensity could be obtained from site-specific observations. Since direct observations concerning water temperature for the entire period were not available, we applied a simple regression model for estimating the water temperature time series based on a site-specific time series of hourly air temperature values.

2. Description of the case study

The ecological and morphological roles of seagrass meadows in temperate shallow coastal areas are widely recognized (Oshima et al., 1999). From the ecological point of view, together with the epiphytic community, they often account for a relevant fraction of the benthic primary production in these water basins. Furthermore, they also give shelter to crustaceans,

fish, and fish juveniles, (Leber, 1985; Pile et al., 1996) thus allowing for the development of highly productive habitats, which are characterized by high biodiversity. From the morphological point of view, their presence stabilizes and oxidizes the sediment and, therefore, represents an important factor counteracting the erosion and reducing the release of ortho-phosphates from the sediment. In the lagoon of Venice, seagrass meadows presently account for the most relevant fraction of the total primary production: 2-3 10^8 Kg of Carbon, 11.7-17.5 10^6 Kg of Nitrogen, and 11.5-17.3 10^5 Kg of phosphorus per year are recycled by means of the seagrass meadows (Sfriso and Marcomini, 1999). Regarding the spatial distribution and composition of the seagrass meadows in the Lagoon of Venice, Rismondo et al. (2003), showed that, in 2002, the most important species was *Zostera marina,* whose pure meadows covered 5% of the total lagoon surface and 40% of the total surface covered by seagrass meadow.

The key role of seagrasses within the Venice Lagoon ecosystem was recognized early and prompted the development of two models (Bocci et al., 1997; Zharova et al., 2001). These models were purposely calibrated for capturing the main features of the seasonal dynamic of *Zostera marina*, but neither was corroborated/validated against independent sets of data. The older model (Bocci et al., 1997) follows the evolution of three state-variables: the density of above-ground shoot biomass, S, the density of below-ground biomass, R, which is composed by roots and rhizomes, and the concentration of nitrogen in shoot biomass, N_S. Therefore, the forcing functions of this model are the time series concerning light intensity at the top of the seagrass canopy, I, water temperature, T_w, and DIN concentrations in the water column and in the interstitial water. However, no references about the sampling site, the sampling methods or the source of the data that were used in the calibration were given in this paper. Therefore, we decided to focus on the second model developed by Zharova et al. (2001)

This model does not take into account the potential limitation of the growth due to the lack of intra tissue Nitrogen, based the findings reported in (Murray et al., 1992; Pedersen and Borum, 1992). As a result, the evolutions of its three state variables, namely the average shoot biomass, P, the below-ground biomass density, R, and the density of the number of shoots, N, are forced only by I and T_w. This feature makes this model suitable for the trend analysis that was outlined in the introduction. The state equations of the model are given in Table 1 together with the functional expression, while the parameters that were used in the original papers are listed in Appendix. As one can see, the production of new shoots, see eq. 2, is inhibited above a certain values of the above ground biomass S, which is obtained by

multiplying the average shoot weight, P, by the shoot number, N. This threshold, namely the parameter σ, therefore represents a sort of "carrying capacity".

3. Methods

The investigation of the long-term dynamic of the *Zostera marina* biomass required the execution of two preliminary phases, namely the estimation of the forcing functions and the partial recalibration of the model. In the first step, the time series of solar radiation intensity, I_0, and air temperature, T_a, which were collected on an hourly basis at the weather station shown in Figure 1, were used for estimating the time series of the input functions such as the daily average incident light at the top of the seagrass canopy, I, and the daily average water temperature, T_w. In the second step, the model was recalibrated, to fit the time series of the above and below ground biomass densities and shoot number density which were collected at the sampling site shown in Figure 1 and presented in Sfriso an Marcomini (1997, 1999). It was necessary to recalibrate the model, which had actually been applied in order to simulate the same set of observations because in Zharova et al. (2001) the input functions had been obtained by interpolating the light intensity and water temperature data which were measured every fortnight at the biomass sampling site. The recalibrated model was then run by using the seven-year long time series of estimated I and T_w as inputs.

3.1 Estimation of the forcing functions

The time series of the daily intensities of the solar radiation at the top of the seagrass canopy, $I(t_k)$, and of the daily average water temperatures, $T_w(t_k)$, were estimated for the period 1/1/1994-31/12/2002. The first input series was estimated by using the following equation:

$$I(t_k) = I_0(t_k) \exp(-EXT\, z) \qquad (1)$$

In Eq. 2, t_k represents a given day, $I_0(t_k)$ is the average daily light intensity, which was computed on the basis of the hourly observations recorded at the weather station in Figure1, *EXT,* is the average extinction coefficient and z is the average depth of the water column. The values of these two parameters were given in (Zharova et al., 2001).

The estimation of the daily water temperatures was less straightforward since the real-time monitoring of this and other water quality parameters by means of automatic probes in the Lagoon of Venice started only in 2002. A preliminary analysis of these data, which were kindly provided by the Venice Water Authority Anti-Pollution Bureau, showed that the lag-0

cross-correlation between the water temperature and air temperature time series which was collected at the weather station was highly significant. This finding suggested that the water temperature could be estimated by using a linear model:

$$T_w(t_k) = \beta_0 + \beta_1 T_a(t_k) \qquad (2)$$

in which $T_a(t_k)$ and $T_w(t_k)$ represent, respectively, the average air and water temperature on day t_k. The regression model was applied stepwise. First, we calibrated the two parameters by using a year-long time series of input and output data and subsequently checked the distribution of the residuals. Based on the results of the analysis of the residuals, the whole set of data was split into two sub-sets and the calibration procedure was repeated. As a result, we obtained two couples of regression parameters, which were used for computing the seven-year long time series of water temperature.

3.2 Model calibration

The model briefly described in the second section was first partially re-calibrated against the time series of the above ground and below ground biomass densities and of shoot density which were collected on a monthly basis from February 1994 to January 1995 in a shallow area of the southern sub-basin of the Lagoon of Venice. These data were sampled within the framework of a comprehensive field study (Sfriso and Marcomini 1997, 1999). The sampling plan included the monitoring of the macronutrients, Nitrogen and Phosphorus, in the water column and in the interstitial water, as well as the measurement of the water temperature and the intensity of the solar radiation at the surface and at the bottom of the water column. These data were used for estimating the extinction coefficient, *EXT*, and the time series of forcing functions that were used in the original paper. Regarding *Zostera marina* biomass, each observation of the time series represents the average of six replicates, which were taken from the same 15x15m square.

The time series of the solar radiation intensity and the water temperature were estimated in accordance with the procedures outlined above on the basis of the meteorological data concerning the same period. These series were different from those used for forcing the model in (Zharova et al., 2001). Based on this consideration, we decided to calibrate the optimal temperatures, T_{opt_phot}, T_{opt_prod}, since the results reported in that paper showed that the model is more sensitive to water temperature than to incident light. Furthermore, a preliminary analysis of the model output indicated that the original value of parameter σ was too low, probably as a result of a printing mistake. Therefore, this parameter was added to the

recalibration set. In order to compare the results of the model with those presented in the original paper, we also estimated the forcing functions using a spline interpolation of the field data, as suggested in (Zharova et al., 2001) and recalibrated the parameter σ also in this case. The *I* and T_w field data were interpolated using a Matlab routine. The calibrations were carried out by minimizing the goal function (Pastres et al., 2002):

$$\Gamma = \frac{\sum_{i,j}(\hat{y}_{i,j} - y_{i,j})^2}{\dfrac{\sum_{i,j}(y_{i,j} - \bar{y}_j)^2}{(n-1)}} \qquad (3)$$

where *i* is the number of observations and *j* the state variable index.

The ODE system presented in Table 1 was integrated numerically using a Runge-Kutta fourth-order method (Press et al., 1987). Field observations of shoot number density and above and below ground biomass densities in February 1994 were taken as initial conditions. The minimum of the goal function (3) was sought by scanning the parameter space, since only three parameters were recalibrated.

3. Results

The regression model (2) was calibrated using the air temperature data measured at the weather sampling stations of the Italian National Research Council from April 1st 2002 to March 31st 2003 as input and the water temperature data which were collected during the same period by the Venice Water Authority as output. The input data can be downloaded at the website *www.ibm.ve.cnr.it,* while those concerning the output were kindly provided by the Venice Water Authority. Calibration results of the regression model for the period April 1st 2002 – March 31st 2003 are summarized in the first row of Table 2 and in Figure 2a, which presents the smoothed time series of the residuals, which was computed by using a centred moving average over the period of a fortnight. As one can see, even though the coefficient of determination was high, the residuals showed that this model systematically under-estimated the data during summertime and early autumn and over-estimated them throughout the rest of the year. Therefore, the water temperature data were fitted by using two sets of parameters: the first set, 1/7/2002-15/11/2002, was calibrated against the summer-early autumn data and the second one, 1/4/2002-30/6/2002 and 15/6/2002-31/3/2003, against the remaining observations. The results of this second attempt are summarized in the second and third row of Table 2, which give the average values of the parameters thus obtained and the coefficient

of determination, R^2, the average and the average sum of squares of the residuals, which were computed using the two models. As a visual inspection of Figure 1b shows, the time series of the residuals thus obtained did not show any systematic deviations from the mean. Furthermore, the mean distance between the model and the observations, i.e., the square root of the average sum of squares of the residuals, were about 1.3 °C in summer-autumn and 1.4°C in winter-spring.

The results of the calibration of the *Zostera marina* model are summarized in Table 3 and illustrated in Figure 3 and Figure 4a-d. The two time series of water temperature used in the recalibrations are displayed in Figure 3. As one can see, the interpolated temperatures were, in general, slightly higher than the average temperatures which were computed using the regression model (2). Table3 gives the values of the recalibrated parameters, the reference values reported in (Zharova, 2001) and the coefficients of determination concerning each state variable. Figure 4a-d shows the time series of the field data and the outputs of the model which were obtained by using as input functions the interpolation of the I and T_w field data and the time series computed as detailed above. In spite of these differences, however, the trajectories here obtained were remarkably similar and, as it was found in the original paper, successfully simulated the evolution of two out of three state variables, namely P and R. These findings suggest that the model is highly sensitive to the water temperature, since the two input time series were slightly different, as Figure 3 shows.

The evolutions of the average shoot biomass, of the shoot number density, and of the above ground *Zostera marina* biomass density during 1994-2001 are displayed in Figure 5. The trends were computed using a centred moving average. A visual inspection of the trends immediately reveals a striking and somewhat unexpected feature. In fact, the trend of the number of shoots density N, showed a marked decrease, which was mirrored by the increase in the trend of the average shoot weight, P. The above ground biomass, S, being their product, increased from 1994 to 1997 and then decreased down to levels similar to those which characterized the first year. The seasonal fluctuations always showed two peaks, but their height and shape were markedly different from year to year.

4. Discussion

The specific results of the partial recalibration and those of the subsequent analysis of the trend of *Zostera marina* biomasses depend on the time series of input functions, which were

estimated on the basis of site specific, high frequency data. Therefore, the question of the reliability of these inputs should be addressed. Regarding the estimation of the light intensity at the top of the seagrass canopy, the measurements of light intensity collected at the weather station represent reliable estimates of the incident light at the surface of the water column because of the short distance between the weather station and the biomass sampling site. Since quantitative information about short-term and long-term variation of the turbidity at the sampling site were not available, the intensity of solar radiation at the top of the canopy had to be computed by using the light extinction coefficient given in (Zharova et al., 2003), which was estimated on the basis of the data collected in 1994-95. This choice certainly represent a source of uncertainty, since the marked increase in the fishing of *Tapes philippinarum* over the last decade (Pranovi et al., 2004) is likely to have caused an increase in the turbidity of the Lagoon from 1994-2001 and, therefore, an increase in the light extinction coefficient. This could have led to an overestimation of light intensity on the canopy and, in turn, of the photosynthetic production. However, even a marked increase in the extinction coefficient cannot account for the marked decrease in the shoot number density since the collapse of the shoot number would only be accelerated by a further decrease in their specific growth rate as a consequence of the increase in the turbidity.

Regarding water temperature, the results summarized in Figure 2 and Table 2 demonstrate that the linear regression between the air and water temperature in the Lagoon of Venice is very strong due to the shallowness of the water column and to the relatively small influence of the heat exchanges with the Adriatic sea. The need of using two sets of regression coefficients, one in winter-spring and the other in summer-autumn, is justified by the analysis of the time series of the residuals but also find explanation in the physical processes which takes place in a shallow lagoon, such as the lagoon of Venice. During the cold seasons, the tidal mixing with the seawater, warmer than the air, mitigates the temperature in the shallow areas of the lagoon. Therefore, the average daily water temperature observed in the lagoon in these periods is higher than the corresponding air temperature. The difference between the average daily air and water temperature becomes very small during summer and early autumn when the water column receive and store large inputs of solar energy. The results of the calibration are consistent with this picture since, in both cases, the intercepts were positive, which means that, on the average, the water temperature was higher then the air at low values of the input variable. However, the slopes were lower than one and very similar, which means that the difference between input and output decreased along with the increase in the input variable. The fact that the average daily water temperature was

always slightly higher that the air should not surprise since the daily fluctuation of the air temperature are much larger than those of the water as a more detailed analysis of the hourly values may show. For example, in the first fifteen days of August 2002 the hourly air temperature ranged from 16.9 to 26.7 °C, while the water ones ranged from 21.9 to 27.9, the average values being respectively 21.9 and 25.0 °C. A further support to the approach here adopted is given by the results displayed in Figure 3. As one can see, the average daily values of the water temperature reproduced the pattern of the field data and, correctly, underestimated them: these were collected during day time, when the water temperature is in general higher than its daily average because of the input of solar radiation.

Overall, the two recalibrations results were satisfactory and showed that the model correctly simulated the dynamic of two out of three state variables, namely P and R, when it was forced using the two water temperature series presented in Figure 3. However, the outcome of the recalibration exercise strongly suggests that the model is very sensitive to the evolution of water temperature. In fact, the two trajectories were remarkably similar as were the two values of the parameter σ. This first finding indicates that the value of σ given in the original paper is not correct, probably because of a printing mistake. However, the optimal temperatures, T_{opt_ph} and T_{opt_prod}, which were estimated by forcing the model using the forcing function computed using Eq. 1 and Eq. 2 were markedly lower than the reference ones, in spite of the slight difference in the input functions, represented in Figure 3. In particular, the shift in the parameters indicates that the position of the biomass peaks is largely determined by the evolution of water temperature (see Figure 4a). This hypothesis is reinforced by the results presented in Figure 6, which shows the monthly average values of the functions $f(T_w)$ and $f(I)$ during the period 1994-2002. As one can see, the solar radiation intensity limits the photosynthetic rate only during a short period in winter time, while the presence of the two biomass peaks in Figure 4 and of the seasonal fluctuations which can be observed in Figure 5 are clearly due to the seasonal fluctuation of water temperature. Figure 4 also shows that the model accurately simulated the seasonal evolutions of the below ground biomass density, which was very similar to that of the above ground one. In fact, above and below biomass peaks occurred almost simultaneously, the only difference being the heights of the peaks. This feature is shared by the field data, at least as far as the summer peak is concerned, and therefore, the results suggest that the transfer of biomass from above to below ground was correctly modelled. The evolution of the density of shoot number, however, did not match the observations as closely as in the case of the other two state variables Figure 4d, but, likewise the data, were characterized by the presence of a summer peak and an autumn

one. Since similar results were also obtained in (Zharova et al., 2001), this finding suggests that this state variable dynamic was not correctly modelled.

From the methodological point of view, the main result of the trend analysis is the discovery that the structure of an apparently “good” model may hide some undesirable features. These features could hardly be noticed when calibrating the model but were easily revealed by the visual inspection of the multi-annual trends of the average shoot biomass P, and of the density of shoot number, N. In fact during the period 1994-2002, the first state variable showed an eleven-fold increase in its level while the second one showed a corresponding eight-fold decrease, as can be seen in Figure 5. As a result, the level concerning the above ground biomass S=PxN at the end of the period is similar to the one that characterized the calibration year, 1994. Such results are not consistent with the observations, particularly as far as the average shoot biomass is concerned since a maximum value of 0.31 g C was estimated on the basis of the available data. This finding points to a fault in the structure of the model, which, combined with the high sensitivity of the trajectories to the inter-annual fluctuation of the water temperature may have originated the trends presented in Figure 5. A more detailed analysis of Figure 5 shows that the marked decrease in the trend of N occurred in the year 1997, which was also characterized by the highest biomass peak. During that year, because of the inter-annual fluctuation of the water temperature, the above ground biomass remained well above the threshold, σ, for approximately 63 days straight horizontal line in Figure 5. During this period, the growth of new shoots was inhibited leading to the marked decrease that can be clearly seen in Figure 5. On the other side, the dynamic of P is not controlled by any factors other than the intensity of solar radiation and the water temperature since in this model the photosynthetic rate is not reduced at high biomass values. Since the first factor counts very little, as Figure 6 shows, the trend concerning P is determined by the value of the parameters μ_{max} and Ω_P and by the interannual variability of water temperature. This formulation is a potential source of instability in the absence of other controls such as predation or nutrients availability.

5. Conclusion

The results presented in the paper suggest that the investigation of the long-term evolution of primary production models under realistic scenarios of forcing functions can easily reveal structural instability that may not be noticed in the calibration phase. In fact, the results of the recalibration showed that the model fitted the field data, but also indicated that it is very

sensitive to small variations in the time series of the water temperature. The results of the trend analysis further supported this finding and clearly showed the presence of potential sources of instability in the model structure. These findings suggest that testing the robustness of primary production model in respect to realistic inter-annual variations of their main forcings, such as solar radiation intensity and water temperature, may add confidence in the results of the calibration. In fact, the calibration does not take into account the wealth of semi-quantitative information about the system dynamic which are somewhat “in the middle” between the theoretical knowledge, represented by the model structure, and the very specific information content of a single, real-world, case-study. As a result, in some instances, this process may lead to successful results, even in presence of some faults in the model structure. The checking process here proposed does not require additional biomass field data and, in the absence of observed time series of these two inputs can be carried out using time series of related variables, as illustrated in this paper. As an alternative, synthetic yet realistic scenarios of input functions could also be generated by perturbing the available data using MonteCarlo methods. Therefore, it provides a simple and inexpensive way of analysing the consistency of the long-term behaviour of primary production models in respect to the interannual fluctuations of non-manageable forcing functions. In the case study presented and discussed here, the long-tem simulation results highlighted the lack of control in the model structure since there was no real feedback between the evolution of the biomass and the biomass itself and the availability of other resources, such as nutrients. Therefore, the dynamic was entirely driven by the non-manageable main input, i.e., water temperature. As a result, the calibration lead to "balance" the positive and negative terms through the estimation of the maximum growth, but the inter-annual variability of the non-manageable drove the system out of control.

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References

Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Philipp, Victoria, Australia. Ecol. Modelling, 118: 131-148.

Beck M. B. (1987). Water quality modeling: a review of the analysis of uncertainty. Wat. Resour. Res., 23(8): 1393-1442.

Bocci, M., Coffaro, G., Bendoricchio G., 1997. Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). Ecol. Modelling, 102: 67-80.

Dejak C., Franco D., Pastres R., Pecenik G. and Solidoro C., 1992. Thermal exchange at air-water interfacies and reproduction of temperature vertical profiles in water columns. Journal of marine systems, 3: 465-476.

Gribble, S.D., 2001. Robustness in complex systems. Proceedings of the 8th workshop on hot topics in operating systems (hotOS-VIII).

Leber, K. M., 1985.The Influence of Predatory Decapods, Refuge, and Microhabitat Selection on Seagrass Communities. Ecol., 66: 1951-1964.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorous limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83-100.

Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. Ecol. Modelling, 115: 19-33.

Pastres, R., Ciavatta, S., Solidoro, C, 2003. The Extended Kalman Filter (EKF) as a tool for the assimilation of high frequency water quality data. Ecol. Modelling, 170: 227-235.

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P., 2002. 'Birthday effect' on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model; J. Mar. Biol. Ass. U.K., 82: 333-337.

Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D. and Dejak C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system; Ecol. Modelling, 138: 231-245.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass Zostera marina during a late summer period of high grow and low nutrient availability. Mar. Ecol. Prog. Ser., 80: 65-73.

Pile, A. J.; Lipcius, R. N.; van Montfrans, J.; Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in Blue Crabs. Ecol. Mon., 66: 277-300.

Pranovi, F.,Da Ponte, F.,Raicevich, S., and Giovanardi, O., 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. ICES Journal of Marine Science, 61: 43-52.

Press W.H., Flannery B.P., Teukolsky S.A., Vetterling W.T., 1987. Numerical Recipes, the art of scientific computing, Cambridge University Press.

Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A seagrass Map for the Venice Lagoon. Proceedings of the Sixth International Conference on the Mediterranean coastal environment, Medcoast 03, E. Özhan (Editor), 7-11 Ottobre 2003, Ravenna, Italy.

Sfriso, A., Marcomini, A., 1997. Macrophyte production in a shallow coastal lagoon. Part I: coupling with chemico-physical parameters and nutrient concentrations in waters. Mar. Environ. Res., 44 : 351-357.

Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II: coupling with sediment, SPM and tissue carbon, nitrogen and phosphorous concentration; Marine Environ. Res., 47: 285-309.

Wortmann, J., Hearne, J.W., Adams, J. B., 1997. A mathematical model of an estuarine seagrass. Ecol. Modelling, 98: 137-149.

Young, P. C., 1998. Data-based mechanistic modelling of environmental, ecological, economic and engineering system. Environmental Modelling and Software, 13: 105-122.

Zharova, N., Sfriso, A., Voinov, A., Pavoni, B., 2001. A simulation model for the annual fluctuation of *Zostera marina* in the Venice lagoon. Aquatic Botany, 70: 135-150.

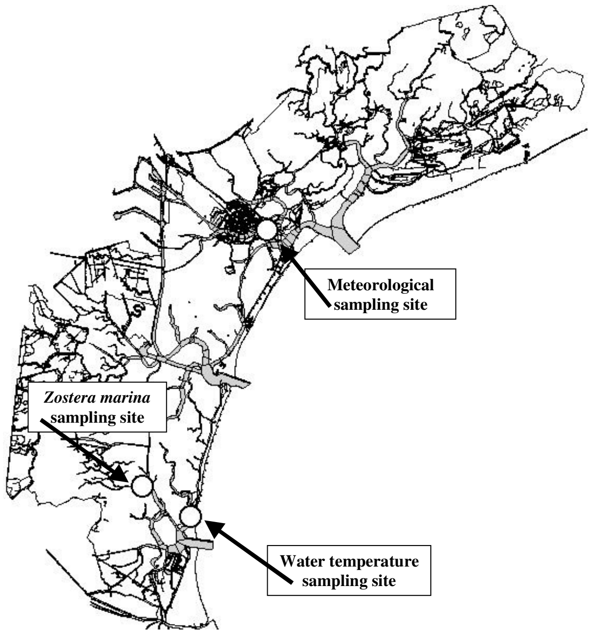

Figure 1. Data sampling sites

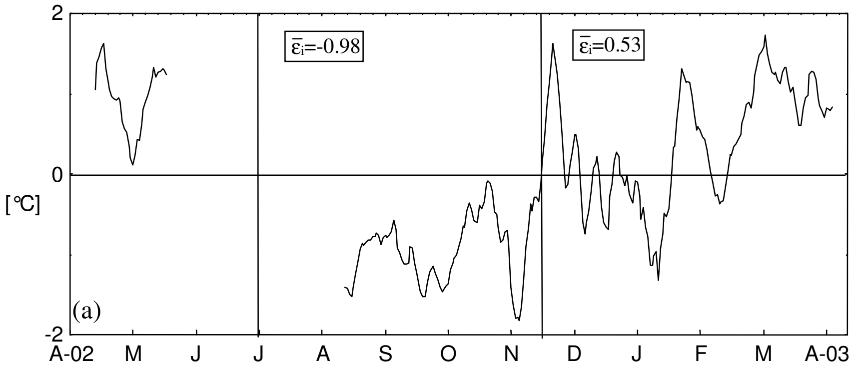

Figure 2a. Smoothed time series of the residuals concerning the application of the regression model to the whole April 2002-April 2003 time series of air and water temperature.

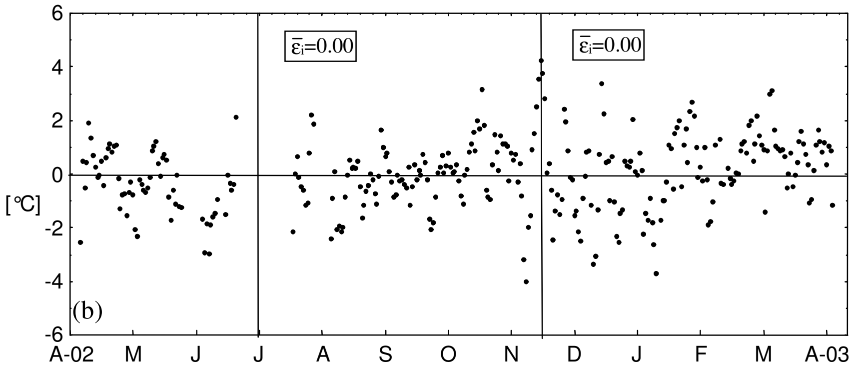

Figure 2b. Time series of the residuals obtained by calibrating the regression model against the summer-autumn and the winter-spring data.

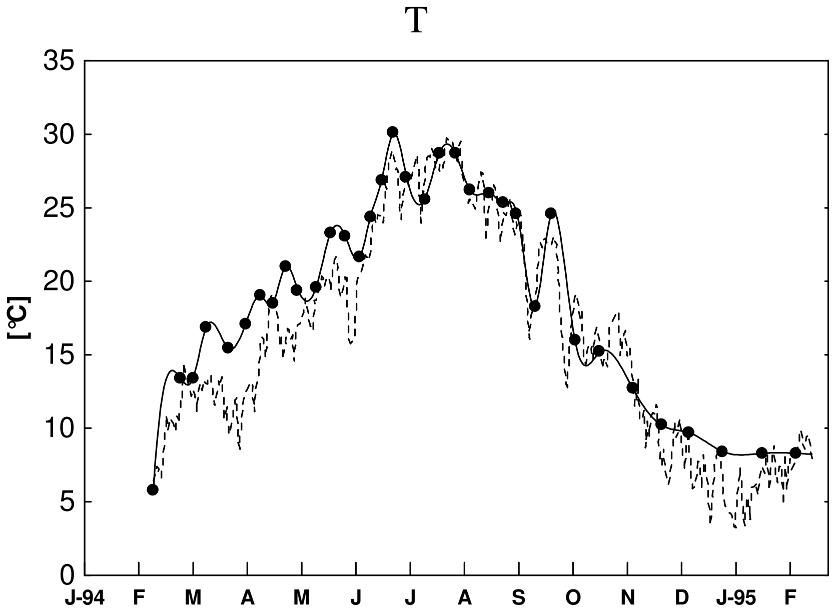

Figure 3. Time series of water temperature estimated by interpolating the field data (continuous line) and the regression model (dotted line).

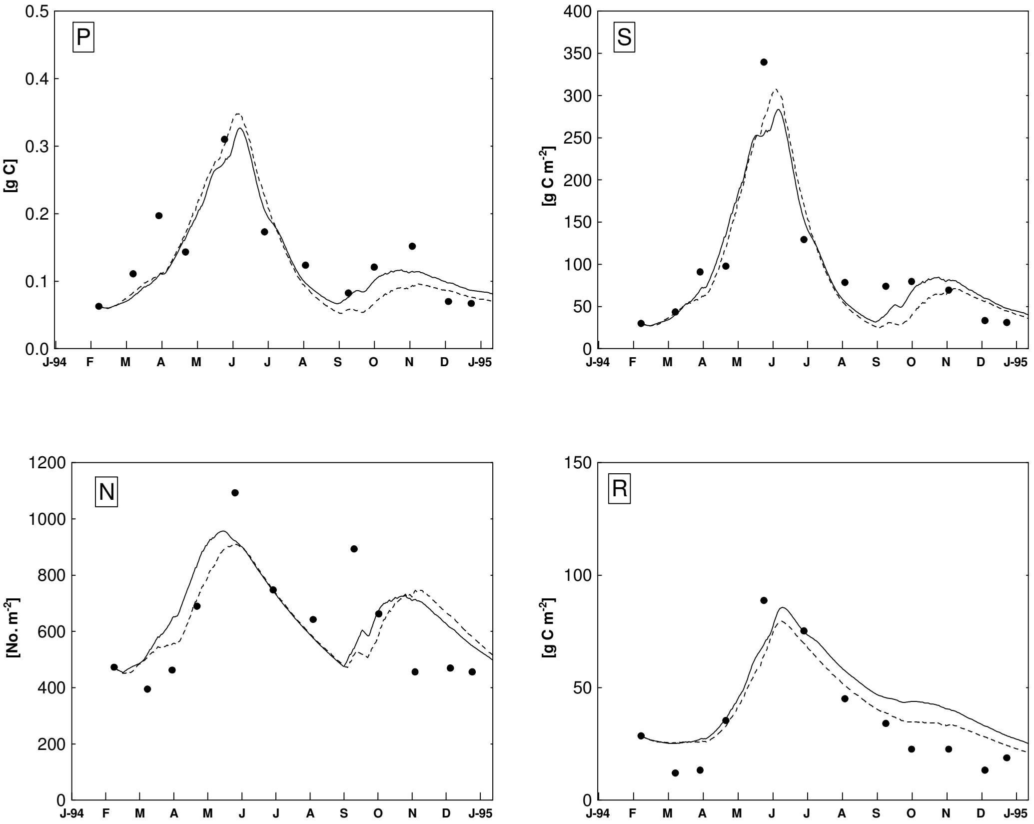

Figure 4a, b, c, d. Comparison between the field data and the outputs which were obtained by recalibrating the model and using the two sets of driving functions: I and Tw interpolated values, continuous line, I and T_w computed by means of Eq.(1) and (2), dotted line.

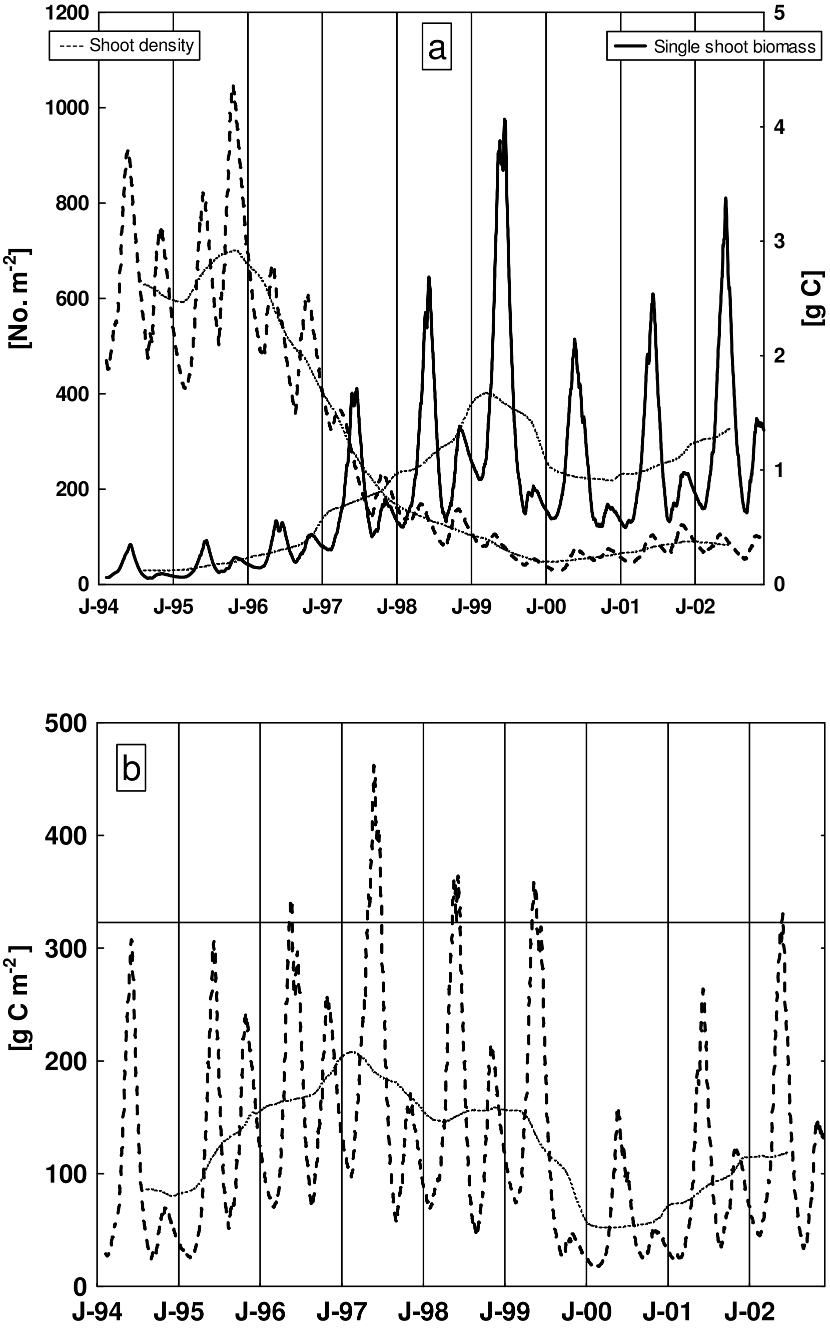

Figure 5. Long term evolution and trend of the density of shoot number, average shoot weight, (a) above ground biomass density S (b). The straight line in (b) represents the threshold σ.

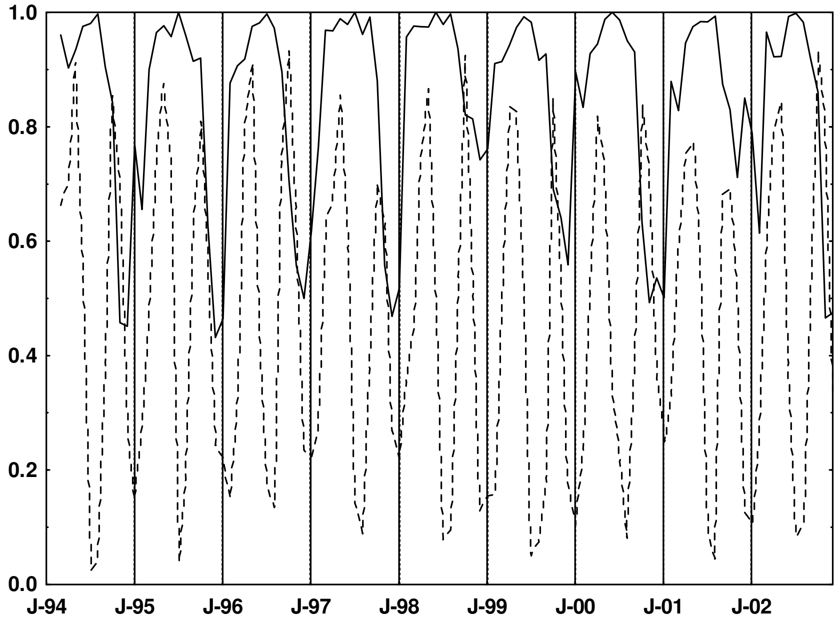

Figure 6. Trends of the average monthly values of the functions which limit the shoot biomass growth in relation to the water temperature $f_{\_phot}(T_w)$ (dotted line) and intensity of solar radiation $f(I)$.

$$\frac{dP}{dt} = P(\mu - \Omega_p) \qquad S = N \cdot P$$

$$\frac{dR}{dt} = trans \cdot S - Pnew \cdot G_N \cdot N - \Omega_R R - \Omega_N R_{up}$$

$$\frac{dN}{dt} = (G_N - \Omega_N) \cdot N$$

$$\mu = \mu_{\max} \cdot f(I) \cdot f_{\_phot}(T_w)$$

$$G_N = GrowN \cdot f(I) \cdot f_{\_prod}(T_w) \cdot f(R) \cdot f(S)$$

$$f(I) = \begin{cases} 0 & I \le I_c \\ \dfrac{I - I_c}{I_k - I_c} & I_c < I < I_k \\ 1 & I \ge I_k \end{cases}$$

$$I_c = I_{c20} \cdot \theta_c^{\,T-20} \qquad I_k = I_{k20} \cdot \theta_k^{\,T-20}$$

$$f_{\_phot}\left(T_w\right) = \begin{cases} k_{0\_phot}{}^{\alpha} & T_w \le T_{opt\_phot} \\ k_{m\_phot}{}^{\beta} & T_w > T_{opt\_phot} \end{cases}$$

$$\alpha = \left(\frac{T_{opt\_phot} - T_w}{T_{opt\_phot}}\right)^{stt\_phot} \qquad \beta = \left(\frac{T_w - T_{opt\_phot}}{T_{\max\_phot} - T_{opt\_phot}}\right)^{stt\_phot}$$

$$f_{\_prod}\left(T_w\right) = \begin{cases} k_{0\_prod}{}^{\gamma} & T_w \le T_{opt\_prod} \\ k_{m\_prod}{}^{\delta} & T_w > T_{opt\_prod} \end{cases}$$

$$\gamma = \left(\frac{T_{opt\_prod} - T_w}{T_{opt\_prod}}\right)^{stt\_prod} \qquad \delta = \left(\frac{T_w - T_{opt\_prod}}{T_{\max\_prod} - T_{opt\_prod}}\right)^{stt\_prod}$$

$$f(S) = \begin{cases} 1 - \left(\dfrac{S}{\sigma}\right)^2 & S \le \sigma \\ 0 & S > \sigma \end{cases}$$

$$\Omega_P = LossP \cdot f\_dec(T)$$

$$f\_dec(T) = \theta_L^{T-20}$$

$$trans = k_{trans} \cdot \mu$$

$$f(R) = \frac{R}{R + \varepsilon}$$

Table 1. State equations and functional expressions of the *Zostera marina* model (Zharova et. al. 2001).

	β_0	$\delta\beta_0$	β_1	$\delta\beta_1$	R^2	$\bar{\varepsilon}_i$	ε_i^2/N
Apr.2002-Apr.2003	2.05	0.2	0.96	0.01	0.95	0.00	2.57
Summer-Autumn (1/7/2002-15/11/2002)	4.29	0.49	0.89	0.02	0.92	0.00	1.63
Winter-Spring	2.44	0.19	0.87	0.02	0.94	0.00	1.87

Table 2. Results of the calibration of the water temperature model.

Forcing functions	Parameter		Calibrated	Ref.	R^2 P	R^2 S	R^2 R	R^2 N
Spline interpolation of in situ I and T_w measurements	σ	gCm^{-2}	281.0	50.0	0.70	0.83	0.66	0.30
Average daily values computed using Eq. 1 and 2	T_{opt_ph}	°C	17.3	21.0	0.59	0.84	0.77	0.27
	T_{opt_prod}	°C	20.0	23.0				
	σ	gCm^{-2}	322.7	50.0				

Table 3. Results of the calibration of *Zostera marina* model.

Appendix A

Parameter	Description	Value and unit	Reference
μ_{max}	Maximum shoot specific growth rate	0.043 day^{-1}	Zharova et al.. 2001
$GrowN$	Maximum new shoots specific growth rate	0.028 day^{-1}	Zharova et al.. 2001
Ω_N	Speficic shoot number loss rate	$7.2\ 10^{-3}$ day^{-1}	Zharova et al.. 2001
$LossP$	Speficic shoot biomass loss rate at T_w=20°C	0.018 day^{-1}	Zharova et al.. 2001
Ω_R	Speficic below ground biomass loss rate	0.009 day^{-1}	Zharova et al.. 2001
k_{trans}	Shoots to roots biomass transfer coefficient	0.21	Zharova et al.. 2001
R_{up}	Uprooting coefficient	0.002 g C	Zharova et al.. 2001
P_{new}	New shoot weight	0.0024 g C	Zharova et al.. 2001
σ	Carrying capacity parameter	50 g C m^{-2}	Zharova et al.. 2001
ε	Half-saturated constant for below-ground biomass	0.0047 g C m^{-2}	Zharova et al.. 2001
I_{k20}	Saturation light intensity at 20°C	25.5 E m^{-2} day^{-1}	Zharova et al.. 2001
I_{c20}	Compensation light intensity at 20°C	2.4 E m^{-2} day^{-}	Zharova et al.. 2001
θ_k	Temperature coefficient for light saturation intensity	1.04	Zharova et al.. 2001
θ_c	Temperature coefficient for light compensation intensity	1.17	Zharova et al.. 2001
z	Depth of the water column	0.7 m	Zharova et al.. 2001
EXT	Light extinction coefficient	0.8 m^{-1}	Zharova et al.. 2001
K_{0_phot}	Value of *fphot(Tw)* at Tw = 0 °C	0.01 day^{-1}	Zharova et al.. 2001
K_{m_phot}	Value of *fphot(Tw)* at Tw = T_{max}	$1x10^{-5}$ day^{-1}	Zharova et al.. 2001
T_{opt_phot}	Optimal temperature for photosynthesis	21 °C	Zharova et al.. 2001
T_{max_phot}	Temperature threshold for photosynthesis inhibition	34 °C	Zharova et al.. 2001
$stt_{\_phot}$	Shape coefficient in fPhot	2	Zharova et al.. 2001
K_{o_prod}	Value of *fprodt(Tw)* at Tw = 0 °C	0.0005 day^{-1}	Zharova et al.. 2001
K_{m_prod}	Value of *fprod(Tw)* at Tw = T_{max}	0.00001 day^{-1}	Zharova et al.. 2001
T_{opt_prod}	Optimal temperature for newshoot production	23 °C	Zharova et al.. 2001
T_{max_prod}	Temperature threshold for inhibition of new shoots production	25 °C	Zharova et al.. 2001
$stt_{\_prod}$	Shape coefficient in fprod	2.5	Zharova et al.. 2001
θ_L	Arrhenius coefficient	1.05	Zharova et al.. 2001

Table A1**.** Parameters used in the *Zostera marina* model.